Meddelelser om Grønland.

Meddelelser om Grønland,

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Commissionen for Ledelsen af de geologiske og geographiske Undersøgelser i Grønland.

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The

Structure and Biology

of

Arctic Flowering Plants.

II.

Udgivet paa Carlsbergfondets Bekostning.

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H. P. Steensby.

Den 19. Oktober ifjor meldte den traadløse Telegraf det sørgelige Budskab fra Atlanterhavet, at Professor Steensby samme Dag var afgaaet ved Døden ombord i Amerikadamperen »Frederik den Ottende« paa Hjemrejsen fra Amerika.

Professor, Dr. phil. H. P. Steensby var født 25. Marts 1875; han studerede Geografi og Naturhistorie, blev cand. mag. i Aaret 1900, Dr. phil. i 1905 paa en Afhandling om Eskimo-Kulturens Oprindelse og i 1911 Professor i Geografi.

Længe før det sidstnævnte Aar havde Steensby udfoldet en betydelig Forfattervirksomhed om ethnografiske, geografiske og anthropologiske Emner og foretaget lange Rejser, men især skal nævnes hans Arbejde for Udviklingen af det geografiske Laboratorium, der nu kan tjene som et Mønster for andre Lande.

BIOLOGICAL

Endelig skal nævnes hans Interesse for den historiske Geografi; hans første Arbejde paa dette Omraade var hans Afhandling om den græske Købmand Pytheas, i hvilken han mente at paavise, at Pytheas var naaet til Ringkøbing-Fjord; hans næste Arbejde paa dette Felt var Afhandlinger om de gamle Nordboers Vinlandsrejser, hvor han følger dem langs Labradors Kyst til selve »Vinland« ved Mundingen af St. Lawrence-Flod. For paa Stedet at konstatere sine Slutningers Rigtighed, foretog han i 1919 en Rejse til de paagældende Egne, og det var paa Hjemrejsen derfra, at Døden indhentede ham.

I 1909 udsendte Kommissionen ham tilligemed Musæumsassistent Thomsen til Kap York paa Grønlands Vestkyst for at studere den derboende Eskimostamme, og Resultatet af denne Rejse foreligger for hans Vedkommende i to interessante Afhandlinger i »Meddelelser om Grønland« Bind XXXIV og L.

I 1913 indtraadte Steensby som Medlem i Kommissionen, hvor han desværre altsaa kun virkede i seks Aar; men paa Grund af hans elskværdige, rolige og saglige Deltagelse i Kommissionens Arbejde og hans levende Interesse for Studiet af Grønland bliver hans Bortgang et stort Tab for Kommissionen.

C. F. Wandel.

8.

Rosaceæ.

By

Knud Jessen.

1913.

In the present paper I have given an account of the growth-forms and of the anatomy of the root, stem and leaf, and also of the flower-biology, of some Arctic and Subarctic *Rosaceæ* in a similar manner to my work on the Arctic *Ranunculaceæ* (vol. 36). — In addition to the alcohol-material in the Bot. Museum in Copenhagen and the herbarium in the same place I have also made use of the literature in order, as far as possible, to collect in one place what is known about these plants.

I wish to convey to Professor Warming my thanks for the readiness with which he has placed at my disposal his notes from his journeys in Arctic Norway and Greenland. Some of the figures are drawn by him and a good many of these have not previously been published. The rest of the figures, with the exception of figs. 8 and 26, have been drawn by myself.

The following species have been investigated: —

Potentilla palustris ..... p. 6.
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Potentilla palustris (L.) Scop.

Lit. IRMISCH, 1861. LINDMAN, 1884. WARMING, 1884. KNUTH, 1894. KÖLPIN RAVN, 1894. NORMAN, 1895. ASTRID CLEVE, 1901. FREIDENFELT, 1904. SYLVÉN, 1906. WOLF, 1908.

Potentilla palustris is widely distributed over a great part of the northern hemisphere. It lives in Arctic and Subarctic regions and extends southwards as far as 40° N. lat.; and the monographer of the *Potentillas*, TH. WOLF (l. c.),

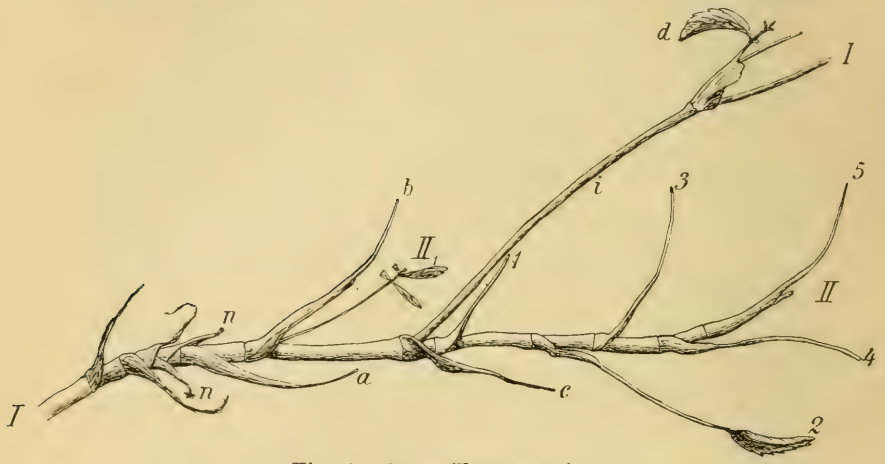

Fig. 1. *Potentilla palustris.*

(Denmark, Oct. 20, 1912; about ½). The leaves are dead. *n, n,* Scale-leaves of the winter bud, 1911—1912; its internodes are slightly elongated; *a, b, c, d,* foliage-leaves on axis I unfolded during early summer; *i,* floral axis; *c* subtends the principal shoot II with the leaves 1—5 which have unfolded during summer; *b* subtends a supplemental shoot ("Bereicherungsschuss").

states that it is highly probable that the species is a remnant of the Arctic tertiary flora and that it has doubtless only recently — perhaps during the Glacial period — advanced southwards. It is everywhere confined to boggy and peaty soil and thrives best at the edge of swamps and high-moors among the peat-forming mosses. NORMAN (l. c.) writes that in Arctic Norway it frequently occurs on the strand and he believes that it is in part distributed by ocean-currents.

The alcohol material on which the following description is based was collected in Greenland and in Denmark.

The figure given of the structure of the shoots of *Potentilla palust.*, illustrates a common feature as regards the shoot-succession when flowering begins. After the winter-bud, which is shown by the short internodes, the first 2—3 elongated internodes of the floral shoot form a continuation of the older axis, while the following internode constitutes the basal part of the ascending branched floral axis. Often even before flowering begins the principal bud grows out, subtended by the leaf (Fig. 1, c) which is seated at the base of the flower-stalk, and forms a sympodial continuation of the axis. But different specimens from the same locality, at any rate in Denmark, may differ greatly as regards the degree of development reached by the principal shoot during the year in which the parent-shoot flowers, in that the length may vary from 2 cm. to about 10 cm., and this proleptic development is by no means a fixed rule even though it is certainly typical in temperate regions. By comparison of herbarium specimens from Denmark, Iceland and Greenland in the Botanical Museum in Copenhagen, it appears, however, to be the rule that the proleptic development of the principal shoot is rarer in the two latter countries than in Denmark, and rarer in Greenland than in Iceland. It was found to be the rule among the Greenland specimens that the principal bud did not emerge until next spring. In vigorous specimens from Denmark, the leaves *a* and *b* in Fig. 1 also often subtend proleptically developed supplemental shoots ("Bereicherungsschüsse") while such were not found in the Greenland specimens in the herbarium, and in only a few of those from Iceland did the leaf *b* subtend a slightly precocious shoot. This proleptic development may perhaps be regarded, for instance, as a weapon in the struggle against the mosses among which *Potentilla palustris* commonly grows; since if the growth in length of the obliquely placed stem was arrested in the middle of summer by the formation of the floral shoot it might easily be overgrown by the mosses.

Furthermore, a more extensive assimilation is attained by the expansion of the new leaves.

Other leaves also may subtend shoots which, however, usually do not grow out until next summer, and it should be mentioned that such shoots which pass their first winter in bud differ in certain respects from vigorous precocious shoots; the latter begin with a more-or-less elongated internode, and the first leaf is a foliage-leaf, so that they can begin to assimilate immediately, while the other shoots begin with 1—3 short internodes and the first 1—3 leaves are scale-leaves.

After germination — probably in the spring — *Potentilla palustris* begins a stage of vegetative growth which lasts for several years. The first year it may form a rosette, but even then may also have elongated internodes (IRMISCH, SYLVÉN, WARMING).

The primary root is slender, but does not die during the first year (WARMING); afterwards the plant is entirely dependent on its adventitious roots which according to IRMISCH arise upon the epicotyledonary axis even during the first year. So far as I have observed they do not arise upon the proleptically developed shoots until during their second summer. The brown, somewhat compressed stem may attain a considerable length; I have dug up sympodia above two metres in length; they may live for at least seven years. As the stem branches freely, vegetative propagation takes place abundantly.

The two-rowed leaves usually live for one summer only, but SYLVÉN says that a single leaf may pass the winter in a green condition. After the leaves have died the large sheaths persist and those seated at the apex of the year's shoot envelop the winter-bud; in the latter a few scale-leaves may also be developed (see Fig. 1).

In Denmark there is no fixed rule as to the height above the surface of the bog at which the shoot-apex lives through

the winter. Some shoot-apices are found raised as much as 10 cm. above the surface, while others are at the surface, and others again are overgrown by the sphagnum of the bog. To judge from specimens in the Copenhagen herbarium it is not a fixed rule for the shoot-apices to die away during winter in Greenland and Iceland, though they no doubt often do so; normally the plant forms a monopodium till flowering begins. In the event of the shoot-apex dying during winter there will always be found a lateral bud upon the stem, situated at the surface of the bog or below it, which can continue the life of the plant.

Irmisch does not understand why this plant is not reckoned among woody plants as much, for instance, as *Vaccinium oxycoccus*, and Warming (1884) very properly calls it a shrub. When *Potentilla palustris* is a chamæphyte it certainly resembles most closely a dwarf shrub, but the case becomes more doubtful when the plant is a hemicryptophyte or helophyte. Sylvén, Th. Wolf and Ascherson and Graebner[1] mention it as an undershrub.

Anatomy. The adventitious roots proceed from the nodes of the stem especially during the second period of vegetation; they branch abundantly, but in each system there is always a well-marked main axis. The anatomy has been treated by Freidenfelt (l. c.). I have, on the whole, found the structure to be the same as that which he describes, but in my material there were no roots with periderm. The epidermis was characterized by being exceedingly small (Fig. 4, *A*); its contents were always brown in colour. In the periphery of the cortex of the adventitious roots of the first order there occur a few layers of cells with slightly thickened walls; intercellular spaces are absent from this part; in the inner part of the cortex the latter are large, and lysigenous lacunæ occur. The endodermis is rather thick-walled. Freidenfelt records that the primary cortex ultimately dies and falls off, a peri-

[1] Synop. d. mitteleurop. Flora. Bd. VI, 1, p. 663.

derm being formed — the latter contains small intercellular spaces — and a secondary woody part. The most vigorous roots in my Greenland material had just begun the development of these structures, but the cortex was living and contained a large amount of starch especially in the part within the exodermis.

In the cortex of the absorbent roots from Greenland fungal hyphæ occurred; these are also recorded by FREIDENFELT in plants from Sweden.

The creeping stem is distinguished anatomically from the floral shoot, partly by its secondary formations and partly by the fact that normally bast is absent from it.

The epidermis of the year's shoot is rather small-celled, the outer wall is about 4.5 μ thick; and the outermost layer of the cortex is slightly collenchymatous. The cortex, in the middle, consists of especially large cells, some of which die at an early period, forming large lacunæ separated by radiating trabeculæ. The cortex of the floral stem behaves in the same manner. During the first period of vegetation the cortex of the shoot dies, but it is found attached to the shoot even during the third year. The central cylinder is surrounded by an endodermis. In the floral shoot the several-layered pericycle is transformed into bast tissue, and only in one particular case did I find bast in the rest of the shoot also, viz. in a plant which grew among shrubs and whose annual shoots of the three last years protruded about ½ metre vertically above the surface of the bog.

The periderm is formed in the outermost layer of the pericycle, and even in the first period of vegetation it reaches a thickness of several layers. Moreover it appears to be stronger in Arctic specimens, and while in Denmark, at any rate when young, it probably does not contain cork-cells, in the material from Greenland 1—2 layers of phelloid-cells alternated with one layer of cork-cells, and as many as 6

layers of the latter may occur. The periderm contains fairly large intercellular spaces, which however are always absent from the inner side of the cork-layers. On older parts of the stem the periderm peels off as brown concentric flakes.

During the first period of vegetation of the shoot is formed the greatest amount of the total secondary wood, since often the addition during following years is only a few layers thick. The annual rings are, however, fairly distinct. The structure of the wood is regular, one-layered medullary rays being separated by vessels and tracheids in one to a few layers. Some wood-parenchyma is, however, also present.

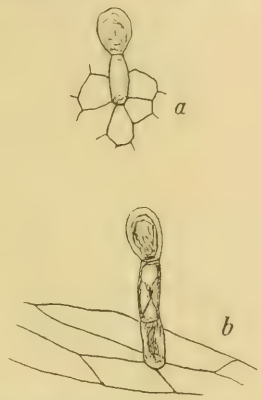

Fig. 2. *Potentilla palustris*. *a* and *b*, Glandular hairs from the lower surface of a leaf from Denmark (Bagsværd); $^{220}/_{1}$.

The pith is heterogeneous. It consists of a broad peripheral part of homogeneous living cells which lasts during the life of the shoot, and in addition of a central part which dies away early. The pith, the medullary rays, the pericambium and the phelloid tissue are the chief depositories of food-material, and during autumn they are filled with starch, but on investigating the shoots in November it will be found that almost all the starch has disappeared and has been replaced by fat the presence of which is indicated by use of Sudan III. In Denmark this change takes place in October.

The imparipinnate leaves are covered on both sides to a greater or less degree with hairs of the usual unicellular form; older leaves are often almost glabrous. Irmisch (l. c.) writes that in the young plant the leaf-stalk and the margin of the leaves bear stalked glands, and on older plants he found such glands also on the leaves which had developed during spring, while they were absent from the leaves which

had unfolded later in the summer. In the neighbourhood of Copenhagen I found in spring numerous glands upon both sides of the leaf (Fig. 2) and upon the leaf-stalk of *Potentilla palustris*, but they were wanting later in the summer, probably they had then fallen off. With the exception of a few specimens, leaf-glands were entirely absent from the Greenland plants which have been investigated.

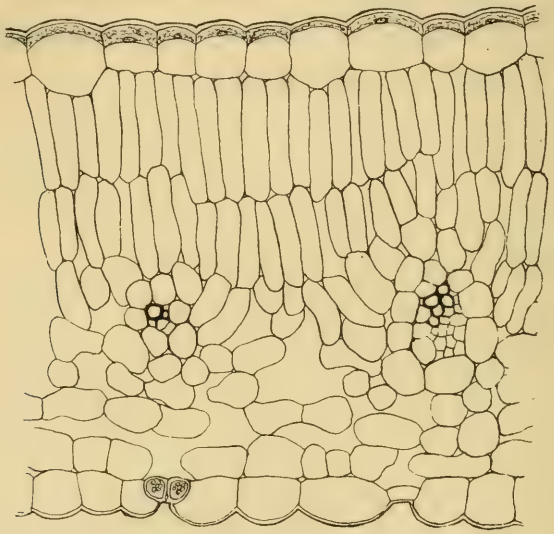

Fig. 3. *Potentilla palustris.*
Transverse section of leaf from Ivigtut in South Greenland ($^{260}/_{1}$). The inner wall of the epidermis of the upper surface is highly mucilaginous.

The under side usually presents a greyish blue colour; this is perhaps due to a thin, granular covering of wax, which must, in addition to the hairs, serve to prevent the under side, which is rich in stomata, from getting wetted.

Stomata may also be found on the upper side; they then occur either singly or in groups (Fig. 4, *C*). The stomata are sunken (Fig. 3). The upper side is slightly reticulated and the outer wall of the stout epidermis is not specially thick, about 2.5 μ; the inner wall is highly mucilaginous (Fig. 3). The

palisade parenchyma usually consists of two layers which may be more or less strongly developed: the leaf figured has a relatively compact structure. The spongy parenchyma is rather loose in structure (Fig. 4, *B*), and a slit-like lacuna is often found within the subepidermal layer. No stereom proper is present in the leaf, only along the main bundle some bast occurs.

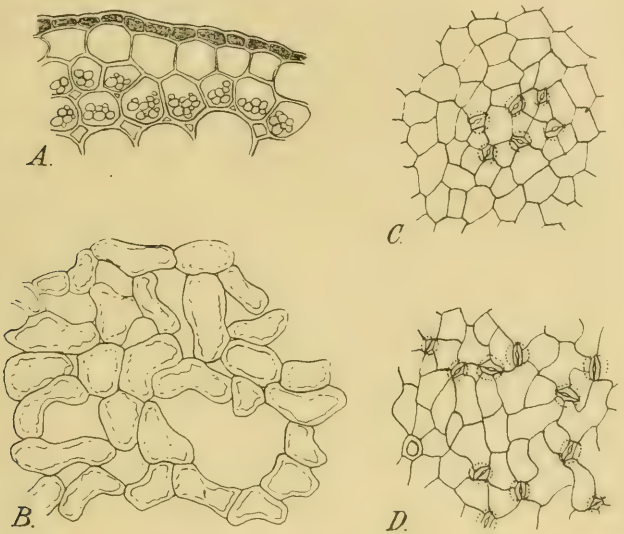

Fig. 4. *Potentilla palustris.* (From Ivigtut in South Greenland). *A*, Epidermis and the outermost layer of cortex of an adventitious root of the first order; the epidermis is about 6.5 μ high. *B*, Section of the spongy parenchyma of the leaf. *C*, Epidermis af the upper and *D* of the lower surface of the leaf. (*A*, *B*, $^{250}/_{1}$; *C*, *D*, $^{130}/_{1}$).

At the apex of the leaf-teeth there are hydathodes with water-stomata on the upper side of the teeth.

The dark brown flower is about 25 mm. in diameter (Knuth); the petals are small, about three times as short as the sepals. It is usually stated that the petals persist while the fruits are ripening (e. g. by Irmisch, Lindman, Knuth and Neuman in "Sverige's Flora"), the sepals after pollination closing round the inner parts of the flower, but

TH. WOLF, on the other hand, states that they fall off after flowering. The flower-biology has been exhaustively described by HEINSIUS[1] and KNUTH (l. c.) from Holland and from the North Frisian Islands respectively; unfortunately my Greenland material contained only a very few flowers, but they corresponded with the descriptions of the above authors in being decidedly proterandrous. According to KNUTH *Potentilla palustris* behaves as follows: Shortly after the young flower has expanded, the extrose anthers on the numerous erect stamens open; when the anthers have fallen off the filaments bend outward toward the calyx and the corolla so that room is made for the stigmas which are now furnished with small, yellow stigmatic papillæ. The flowers are eagerly visited by bees. Honey is secreted by a green disk between the carpels and the stamens; this had already been observed by KONRAD SPRENGEL. NORMAN writes that the great amount of honey contained in the flowers attracts numerous insects, flies, butterflies and bees, which continue to visit the flower a long time after fertilization has taken place.

The time of flowering is in Central Europe in June and July; in Arctic Norway it begins about July 20; in the mountains of northern Sweden it is recorded to be in August, in Greenland in July and August. In specimens from Denmark I found young flower-buds in the beginning of May, while such were not found in the middle of March. So the flower-development probably begins at the same time as the closely folded winter-bud begins to open. In some of the northernmost localities of Arctic Norway it may happen that flowers are not developed. Miss CLEVE found no fruit in the mountains of northern Sweden.

The theory advanced by NORMAN that in the coastal districts of Norway *Potentilla palustris* is dispersed by marine currents is borne out by the fact that the fruit is

[1] Bot. Jaarboek, 1892, Tab. II, figs. 7—9.

certainly able to float. This point has been discussed by Kolpin Ravn (l. c.) among others. He found that the fruits keep afloat even while they are germinating, and anatomical investigation showed that the thick testa consists of several layers of cells, which contain air. The inner part of the pericarp consists of protective stone-cells.

Potentilla tridentata Soland.

Lit. Hartz, 1894; Wolf, 1908.

This plant grows in Greenland, Arctic North America, Labrador, Newfoundland and Canada. It occurs in clefts of rocks, on lichen-heaths and in other dry localities.

The alcohol material was collected in the following localities in Greenland: Christianshaab, Ivigtut, Sukkertoppen and Holstensborg.

Lange and Wolf call *Pot. tridentata* an undershrub, and as is the case in *Potentilla palustris* the lignified axis lives several years. It is a typical wandering plant with a horizontal, richly branched rhizome from which slender adventitious roots arise. Usually the runners, which may be above 30 cm. long, are etiolated and bear scale-leaves, but creeping shoots with elongated internodes, bearing only foliage-leaves, are also met with; such epiterranean shoots may also be ascending. The scale-leaves are distichous. The shoots which arise from the runners and which often grow out from older stems have probably a life-cycle of several years. In the first period of vegetation they are wandering and pass the winter with straight apex, and not until the second period or perhaps even later do they enter the rosette-stage and form foliage-leaves. It appears to be necessary for the young rosettes to pass through a stage of vegetative growth before they attain the flowering stage. The apex of the rosette-shoot is protected during winter by the large, closely folding sheaths of the older leaves; scale-leaves are

probably not developed (Fig. 5,A, B ,C). The foliage-leaves probably remain green during winter; when they die the three leaflets fall off separately, and the stalk persists (Fig. *A*). The floral shoot is terminal and the principal bud arises in the axil of the uppermost rosette-leaf; it begins with a small transversly placed scale-leaf, and opens its first foliage-leaf in the year in which the parent-shoot flowers. As other lateral shoots may be developed in the rosette, the plant

Fig. 5. *Potentilla tridendata.*

A, Flowering rosette-shoot; *i*, floral axis; the principal bud II is borne in the axil of the uppermost rosette-leaf, the dead leaf-stalks are seen below the fresh leaves. *B*, Drawn from a herbarium specimen; a scale-leaf upon an older and now flowering shoot subtends a new runner. *C*, Apex of a runner. *D*, Carpel; the ovaries are hidden by long hairs. *A*, *C* are from Ivigtut, 20. 8. 1883; *B* from Ivigtut, 1868; *D* from Præstefjæld (*A*, *B* and *C* about natural size; *D* $^{12}/_{1}$).

may form loose tufts. The floral axis bears a few foliage-leaves below the often profuse inflorescence.

ANATOMY. Only older adventitious roots have been investigated. The phelloid of the periderm contains, as in the rhizome, scattered thick-walled wood-cells. The cells of the cork-layers are rather thick-walled. The intercellular spaces are fairly large.

The young runner is protected by a strong epidermis the outer and inner walls of which measured 4.4 μ and 3.5 μ respectively. The outermost layer of the cortex is also fairly

strong, but otherwise the thick cortex is rather loose and perishes early. The central cylinder which is surrounded by an endodermis contains only a few primary bundles and a homogeneous pith of long duration. A continuous cambium develops during the first period of vegetation a considerable amount of wood as in *Pot. palustris*. This — the secondary wood — consists, in addition to large vessels, of one-layered medullary rays usually one layer high, and also of about equal quantities of thick-walled stereom-cells and woody parenchyma. Some indistinct annual rings may be distinguished in the older rhizomes which may attain an age of at least about ten years. The periderm is thick and consists of series of layers of usually 3-layered phelloid separated by one layer of cork. The outer tangential wall of the cork-cells is especially very thick. Some of the older phelloid-cells in rhizomes from several localities had very thick walls which were lignified (Fig. 6, H). These strengthening cells form connecting bands between the vigorous cork-cells in the periderm and probably thereby delay the peeling-off of the latter. There are large intercellular spaces in the periderm; these are, however, absent from the inner side of the corky layer.

The often rather tall flowering shoot is stiffened partly by a strong bast cylinder situated outside the sieve-tissue, and partly by the secondary wood formed by a continuous cambium the peripheral part of which consists chiefly of thick-walled tracheids. The tangential walls of the epidermis are strong, the outer one measured 4.5 μ and the inner 3.3 μ. The outer layers of the cortex are somewhat collenchymatous and as the otherwise loose cortex is rather few-layered, the outer stereom-ring is close to the periphery of the stem. An endodermis is present.

The pith consists of a narrow, small-celled peripheral part formed of living cells only, and a larger central part consist-

ing of larger cells of which a greater or smaller number often dies, but nevertheless the shoot cannot be called hollow.

The leathery leaf, which is 238—270 μ thick, has a decidedly xeromorphic structure in correlation with the fact that the plant grows in dry localities; perhaps it also may live through the winter. It is glabrous upon the upper surface, but upon the lower surface it bears in addition to scattered adpressed hairs of the common type also numerous glandular hairs of two other forms (Fig. 6, E, F.). In the smaller form the apical cell is almost spherical and in the larger ovate to cylindrical. The stalk is often several-celled. These hairs spring from epidermal cells which are smaller than the rest and have a thin outer wall. Perhaps these hairs with their thin-walled and plasma-filled apical cells are able to absorb water which may then be carried into the leaf. Both the upper and lower epidermis have very strong outer walls; thus that of the upper surface measured between 8 and 11 μ and that of the lower about 11 μ. The lower surface of the leaf is moreover highly reticulated. The lower epidermis in particular has a strong cuticle which is somewhat rough. The epidermis of the upper surface is characterized by its tangential walls being mucilaginous to a very high degree, especially the inner; the mucilaginous covering is always wanting above the larger bundles. (Fig. 6, A.). Both leaf-surfaces bear stomata, but upon the upper surface they are very scattered and are surrounded by a group of smaller cells (Fig. 6, B). Upon the lower surface they are placed closely and are not definitely arranged. They are sunk below the level of the surface (Fig. 6, *A*). The radial walls on both the upper and lower surface are only slightly wavy; they are highly perforated on the lower surface (Fig. 6, *C*); on the upper surface the pores occur in larger quantities only near the bundles.

The palisade parenchyma occurs in 2—3 layers of closely

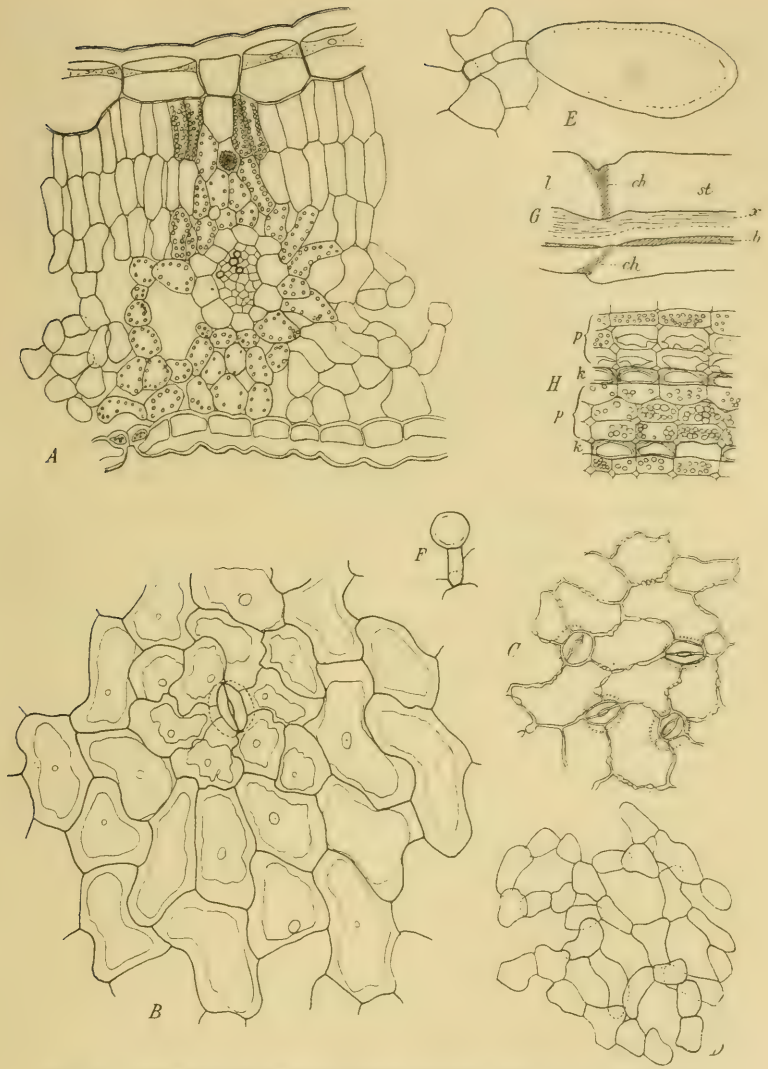

Fig. 6. *Potentilla tridendata* (From Christianshaab in Greenland).

A, Transverse section of leaf; both the tangential walls of the upper epidermis are mucilaginous. *B*, Epidermis of the upper leaf-surface, a stoma is seen surrounded by small cells. *C*, Epidermis of the lower leaf-surface. *D*, Section parallel to the surface of spongy parenchyma from the middle of the leaf between a pair of bundles. *E* and *F*, Two glandular hairs from the lower leaf-surface. *G*, Longitudinal section of leaf-stalk through the zone where the leaf-blade is cast off; *b*, bast; *ch*, collenchyma; *l*, the basal portion of the leaf; *st*, stalk; *x*, xylem. *H*, Fragment of a transverse section through the periderm of a rhizome; *k*, cork-layer, the striation of the walls is not so distinct as shown in the figure; *p*, phelloid-cells; the upper side is the outer. (*A*, *B*, *C*, *D*, *E*. *F* and *H* $^{220}/_{1}$; *G* $^{18}/_{1}$).

placed narrow cells, which to a certain extent are grouped around the bundles. The proportion between the thickness of the leaf and the thickness of the palisade parenchyma is about $\frac{2.4}{1}$. The spongy parenchyma is built in such a manner, that between the bundles in the middle of the leaf areas occur where the intercellular spaces are very large. This structure has this effect that the thick, solid leaf succeeds in getting a well-developed system of larger canals in the respiratory tissue[1]. For the rest the spongy parenchyma consists of rather small cells of simple form (Fig. 6,*D*).

The larger vascular bundles are accompanied by bast both upon the upper and the lower surface. The leaves are very rich in sphaero-crystals which occur especially along the bundles.

When the trifoliolate leaves die, the leaflets fall off separately, as mentioned above, and leave a scar upon the leaf-stalk which persists upon the rhizome for a year or more. Fig. 6, *G* shows a median, longitudinal section through a leaf-stalk just below the blade. The leaf-fall is in several ways prepared for through the anatomical structure. The three bundles of the leaf-stalk divide, so that three enter each leaflet. The bundles of the median leaflet are all of almost the same strength, and lie in almost the same plane; in the lateral leaflets the two lateral bundles are very small. In the zone where the leaflet is to be thrown off there is no bast along the bundles, as is the case both in the leaf-stalk proper and along the main bundles of the blade, and the zone in question is further distinguished by a collenchymatous area which extends straight through the stalk. In the peripheral part of the collenchymatous area the direction of the line of separation is indicated by the longitudinal direction of the cells; thin-walled areas further facilitate the falling process.

[1] Cf. *Coptis trifolia.* Arct. Flow. Pl., I, 6. *Ranunculaceæ*, by KNUD JESSEN; Fig. 58, B. Meddel. om Grönland, Bd. 36.

The leaf-stalk is also stiffened, in addition to the fibrous tissue of the bundles, by some collenchyma which at the angles attains a thickness of several layers. The outer wall of the epidermis is also strong.

The open, cymose inflorescence is few- to many-flowered. The entire petals are white, and the stamens — 20 in number — have very long reddish filaments. The diameter of the flower is 10—15 mm. (Wolf). The flower is scentless; there is a greenish yellow disk around the base of the stamens; the intensely flesh-coloured anthers appear to dehisce before the stigma is functional (Warming's notes). Investigation of about 10 flowers preserved in spirit and collected from different districts in Greenland showed that the minute stigma of the long styles does not bear papillæ even in flowers which were so old that the anthers had fallen from the filaments. In spite of a close search I found only one pollen-grain upon a stigma; among the crowded long hairs of the gynophore much pollen is usually found in older flowers. The anthers form pollen abundantly, which is, apparently, capable of germination. Warming states in his notes that in some inflorescences from the previous year from different localities in Greenland he found a few fruits which appeared to be ripe. Hartz (1894) found *Pot. tridentata* in flower on Præstefjæld on June 15, 1890; the flowering is continued into September.

Potentilla pulchella R. Br.

Lit. Andersson and Hesselman, 1900. Simmons, 1906. Wolf, 1908. Lundager, 1912.

This is a purely Arctic species; it grows in Spitzbergen, Greenland, Arctic North America and on Wrangel Island off N. E. Siberia. Its habitats are rocky and grassy flats. — The alcohol material I had for investigation was from Snenæs in N. E. Greenland and Tempel Bay in Spitzbergen.

Pot. pulchella has a vigorous multicipital primary root, which may attain a considerable length — about 30 cm. or perhaps more — and probably lives as long as the plant; adven-

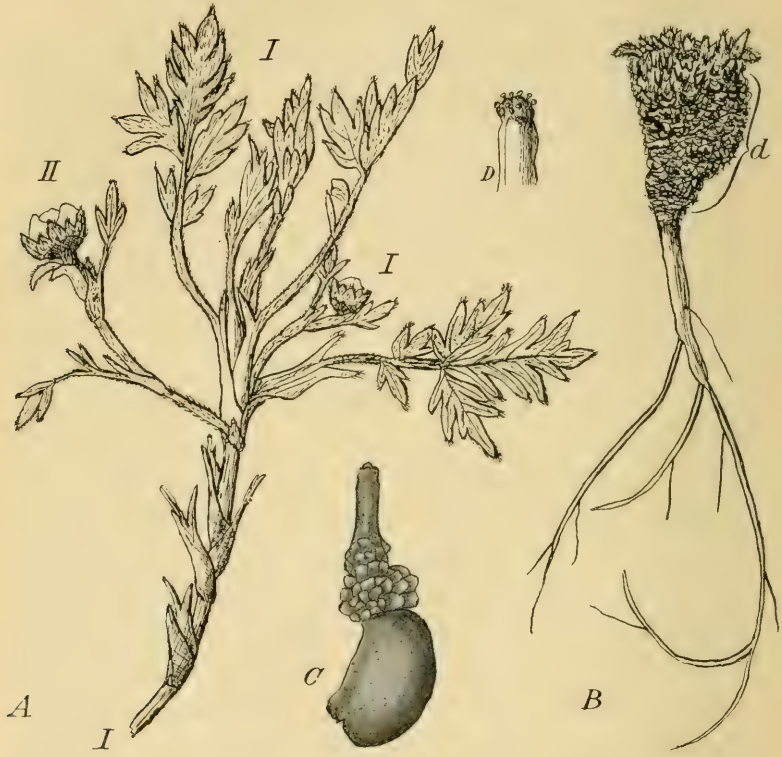

Fig. 7. *Potentilla pulchella* (From Snenæs in Greenland).

A, Shoot with internodes elongated to an unusual degree; *I—I*, the monopodial main axis bearing in its basal part dead fragments of leaves from the previous year; *II*, flowering lateral axes (12. 7. 1908; the upper floral axis is wrongly marked *I*); about natural size. *B*, *f. humilis*; *d*, closely packed dead fragments of leaves; at the top the living leaves form a layer a few mm. in height (22. 6. 1908); about natural size. *C*, Pistil which has not as yet received any pollen; $^{25}/_{1}$. *D*, Fragment of a style with stigma upon which are germinating pollen grains; $^{25}/_{1}$.

titious roots are probably not developed. The often numerous, rosette-leaved shoots are usually very close-set, and solid tufts of considerable size (about 20 cm. in diameter) may be formed. The new leaves project between the crowded

old leaves and their remains. The older portions of the stems appear ultimately to become bared (Warming's notes). The prostrate floral shoots (Th. Wolf) are lateral (Fig. 7, *A.*); their subtending leaves are often dead when they flower, so that they arise from the stem below the terminal rosette. The leaf-sheaths are large and closely folded around the young leaves at the apex of the stem. I found no scale-leaves. The much divided leaves are densely hairy especially in Lange's *f. humilis*, the leaves of which bear long close-set hairs on both sides, while his *f. elatior* is only slightly hairy upon the upper surface. Lundager (l. c. p. 406) writes regarding *f. elatior* that on Lille Snenæs in N. E. Greenland it was found along river banks, and had very long roots which might reach a length of 1.15 metre "and to a great extent were lying so high that a portion of them lay bare." On the other hand, he found *f. humilis* on gravel-banks exposed to the wind and so greatly influenced by the sand-drift that they acquired columnar forms, "pillars," as shown in figures 7, *B* and 8.

Anatomy. The very slender absorbent roots contain fungal hyphæ in the large-celled, few-layered cortex. The epidermis dies early and collapses; the same happens to large portions of the cortex with the exception of the exodermis and the cell-layer outside the strong endodermis. The structure of the exodermis is specially strong, its radial walls, especially on the outside, being highly thickened in the same manner as in *Pot. emarginata.* Secondary growth in thickness begins early in the roots and also the formation of periderm. Usually I found in the lateral roots a continuous woody portion with scattered vessels, but in these roots the woody portion may also be divided into radiating parts separated by broad non-lignified medullary rays. This is what happens in the primary root, and owing to this structure and also on account of its considerable thickness (5—6

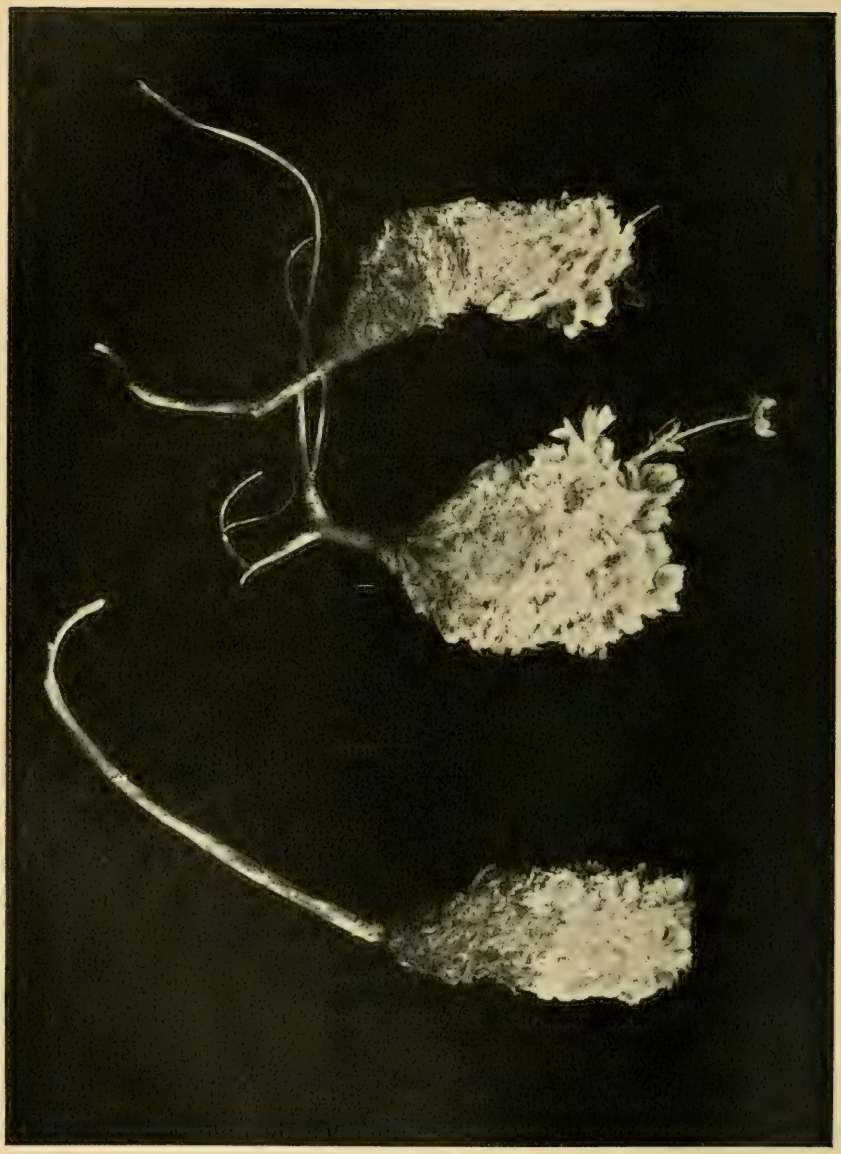

Fig. 8. *Potentilla pulchella*; "pillars" from N. E. Greenland (Nat. size).
(From *C. H. Ostenfeld* and *Andr. Lundager*: List of vascular plants from N. E. Greenland. "Meddel. om Grønland", XLIII, København, 1910).

mm.) it becomes a spacious reservoir of food-material. A plant collected on Snenæs in the middle of June contained in the primary root in addition to some starch large quantities of fat. The walls in the older secondary cortex are collenchymatous and the tissue has the appearance of being highly compressed. — The periderm around the roots does not attain any considerable thickness (about 10 layers) and consists of alternating layers of cork and phelloid. Small intercellular spaces occur between the phelloid-cells, but there are probably none upon the inner side of the cork-layers.

The structure of the rhizome is similar to that of the primary root, the vessels being gathered into rays rich in parenchyma and separated by broad non-lignified medullary rays (Fig. 9, *G.*). Distinct annual rings were not observed either in the rhizome or in the primary root. The pith is large and persistent; it contains large intercellular spaces. The secondary cortex becomes compressed by the growth in thickness; the walls are somewhat collenchymatous. In the young rhizome there is an endodermis. The periderm consists of layers of cork and phelloid-cells which alternate; it does not attain any considerable size (about 8 layers). Intercellular spaces occur as in the root. In a rhizome collected on July 12 on Snenæs (N. E. Greenland) in addition to some small-grained starch a considerable amount of fat was found in all the living tissues.

The flower-stalk contains about 10 vascular bundles; no continuous cambium is developed. There is no endodermis proper. In the older stalk the several-layered pericycle is probably transformed into bast; but my material contained young stalks only. The few-layered cortex consists of an inner part with large cells without chlorophyll and an outer part with chlorophyll; in the latter the outermost cell-layer is slightly collenchymatous. The outer wall of the epidermis is about 3 μ thick. The pith is homogeneous.

Fig. 9, *A* shows that the leaf-margins may be revolute, which is especially the case in *f. humilis;* and the tomentose hair-covering of the lower surface is a good protection for the leaf against the danger of excessive transpiration. Both

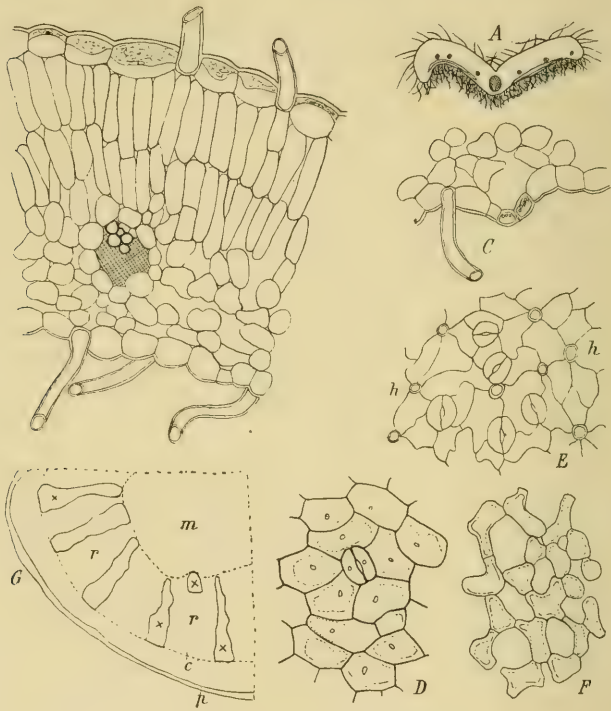

Fig. 9. *Potentilla pulchella.*

A, Transverse section of a leaf-segment. *B*, Fragment of a transverse section of a leaf of *f. elatior*, the inner wall of the upper epidermis is highly mucilaginous. *C*, Stoma from the lower surface of the leaf. *D*, Epidermis of the upper and *E* of the lower surface of the leaf; *h*, the base of a hair. *F*, Section of spongy parenchyma parallel to the surface. *G*, Fragment of transverse section of rhizome; *c*, cambium; *m*, pith; *p*, periderm; *r*, medullary rays. *x* xylem. A, From Tempel Bay in Spitzbergen: *B*, *C*, *D*, *E*, *F* and *G* from Snenæs in Greenland (*A* and *G* about $^{16}/_{1}$; *B*, *C*, *D*, *E* and *F* $^{190}/_{1}$).

leaf-surfaces have scattered glandular hairs. Upon the upper surface only a few stomata occur which are situated on a level with the leaf-surface; the numerous stomata upon the lower surface are on the other hand usually slightly projecting

(Fig. 9, *C*.). The outer wall of the upper epidermis in *f. elatior* is 2.5—3.5 μ thick; in *f. humilis* from Lille Snenæs it was found to be about 6.5 μ; the inner wall is mucilaginous (Fig. 9, B); the radial walls are straight (Fig. 9, *D*); in the lower epidermis they are wavy (Fig. 9, *E*). In the palisade parenchyma also a difference was found between the two forms, there being 2 layers in *f. elatior* (Fig. 9, *B*), but 3 layers in *f. humilis*, which is on the whole somewhat more xeromorphic. The spongy parenchyma is rather loosely built and consists of somewhat branched cells (Fig. 9, *F*). Bast either does not occur or is slightly developed only along the strongest bundles.

The yellow petals are slightly longer or according to Simmons usually only just as long as the sepals, and the diameter of the flower is about 10 mm. (Wolf); there are 20 stamens with short filaments. According to the alcohol material from Snenæs in Greenland the species appears to be homogamous. In the young flower which was just opening the anthers were found to be closed, and the short, slightly lobed stigma had not as yet received pollen (Fig. 7, *C*). In an older flower some of the stamens were bending with open anthers inwards towards the pistils, and the appearance of the stigmas was as shown in Fig. 7, *D*; they were densely covered with germinating pollen. Spontaneous self-pollination probably occurs. *Pot. pulchella* flowers in July; in Spitzbergen flowering begins at the end of June and is continued into September. Fruit is set regularly and abundantly (*A.* and *H.*; Simmons).

Potentilla nivea L.

Lit. Bonnier, 1894. Hartz, 1894, p. 6; 1895 a, pp. 287, 300; b, p. 322. Norman, 1895. Kruch, 1897. Abromeit, 1899. Andersson and Hesselman, 1900. Cleve, 1901. Sylvén, 1906. Hollstein, 1907. Wolf, 1808.

This species grows on rocks, and on rocky and grassy flats; it avoids well-aerated moist soils (Cleve). It is circum-

polar and is found in addition in Alpine regions in the temperate parts of Asia, America and Europe.

The alcohol material is from northern Norway and from Greenland.

Pot. nivea has a multicipital main root, which may attain a considerable length, at least 60 cm. (WARMING's notes) and may also become very thick (6 or even 9 mm.). The often numerous shoots are usually short and close-set, so that they form compact tufts which may attain a diameter of at least 20 cm. The shoots are covered by the old, brown leaf-sheaths which, however, disappear in the course of the following years. Sometimes looser tufts are also found; WARMING, in his notes, even mentions short, horizontal shoots. In the Botanical Museum in Copenhagen I have measured obliquely ascending shoots which were about 10 cm. in length. Adventitious roots, which are even fairly strong (about 2 mm. in diameter), are frequently found, and it must undoubtedly be presumed, as WARMING also is of opinion, that new individuals may be formed by vegetative propagation. The floral shoots are lateral; in a small tuft gathered on Danmarks Ø in East Greenland at the end of the winter the young floral shoots were found to be subtended by dead leaves.

The leaves wither in the autumn, but in favourable localities in southern regions a few small new leaves may protrude a little before the winter owing to the fact that the plant has no real winter-bud with scale-leaves. According to HARTZ, in Scoresby Sound in East Greenland it lives through the winter in places free from snow.

Anatomy. The absorbent roots contain fungal hyphæ in balls in the cells of the few-layered, loosely built cortex. The structure of the epidermis and the exodermis is as in *Pot. emarginata;* but the walls of the exodermis are somewhat weaker than in the latter species. In the primary root the secondary woody portion is at first continuous, and not

until the roots get somewhat older are the broad non-lignified medullary rays developed. The periderm is not very thick: in it one layer of cork-cells alternates with one layer of phelloid-cells. The older secondary cortex becomes highly compressed and is somewhat collenchymatous.

The rhizome, with the exception of the periderm, has a structure similar to that in *Pot. pulchella*. In the periderm one layer of phelloid-cells alternates with one layer of cork-cells, as in the root. The inner cellulose-layer of the phelloid-cells is fairly strong. An endodermis is present in the young rhizome. The structure of the rhizome from Dauphiné, as described by Hollstein, is similar to that of the present one. Hollstein writes that the outermost layers of the phloem is somewhat collenchymatous, and I find this generally to be the case in the greater part of the area between the cambium and the phellogen, but the peculiar appearance cannot be explained solely by this fact; it is no doubt chiefly due to a strong radial pressure.

The rhizome together with the primary root is the chief depository for food-material; and I find the alternation in the abundance of starch and fat according to the season of the year to be the same as is indicated in *Pot. emarginata*. The materials contained in the rhizome in five different months from somewhat different localities in Greenland varied as follows: —

	18. II. 92.	10. IV. 92.	31. V. 08.	1. VIII. 07.	4. XI. 91.
Starch.	a little.	0.	0 to rather much.	much.	0.
Fat.	much.	rather much.	a little.	very little.	rather much.

The plants gathered in November, February and April were from Danmarks Ø in East Greenland, while the plants gathered in May and August were from other localities in East Greenland. The quantity of the starch increases during summer till in August all the tissues are crowded; in November the starch has disappeared entirely; in February a small

quantity was, however, present. During summer only a very small amount of fat occurs; during autumn the quantity increases; a maximum is reached about the middle of February, then the amount begins to decrease.

For the structure of the flowering axis the reader is referred to HOLLSTEIN.

The leaves, which are usually tripartite, are covered with a dense felt of white hairs on the lower surface; the

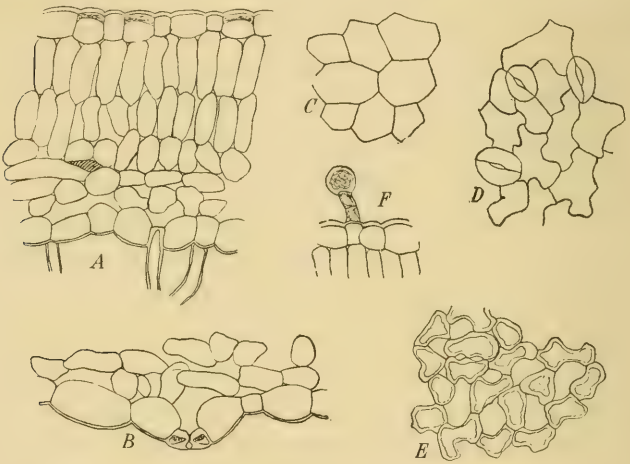

Fig. 10. *Potentilla nivea.*

A, Transverse section of a leaf, a few of the cells of the upper epidermis have mucilaginous inner walls. *B*, Stoma on the lower surface of the leaf; it projects slightly. *C*, Epidermis of the upper surface of the leaf and *D*, epidermis of the lower surface. *E*, Section of the spongy parenchyma of the leaf parallel to the surface. *F*, Stalked gland from the upper surface of the leaf. Kongsvold in Norway. (A, *B*, *C*, *D*, *E*, *F* $^{185}/_{1}$).

upper surface is glabrous or may sometimes be more or less hairy. Fig. 10, *F* shows a glandular hair. Such hairs were found, both on the leaves from Norway, and on leaves of plants in the Herbarium of the Botanical Museum in Copenhagen gathered on Danmarks Ø in East Greenland (HARTZ), at King Point in Arctic America (determined by Dr. OSTENFELD), in the Tyrol (Huter) and in the Altai. The glandular hairs are found on both leaf-surfaces though not in great quantity. There is the more reason for emphasizing this fact as WOLF

(l. c.) in his key of the species in the group *Nivea* states that among others the present species and *P. Vahliana* (see p. 34) are destitute of such hairs. The method for discovering hairs described by WOLF (loc. cit. pp. 32 and 38) cannot be employed with certainty in the case of leaves with a dense layer of felt as in these two species, when the object is to prove the possible presence of glandular hairs; I have demonstrated the hairs in transverse sections.

The leaf-margins are often more or less revolute. The stomata do not occur exclusively upon the lower surface: the few scattered stomata upon the upper surface are situated on a level with the surface, while those upon the lower surface often project slightly (Fig. 10, *B*). The outer wall of the upper epidermis varies in thickness from about 3 to about 4.5 μ, in that of the lower it is about 2.5 μ thick. The radial walls of the epidermis are straight and undulating on the upper and lower surfaces respectively (Fig. 10, *C*, *D*). Several of the cells of the epidermis on the lower surface of the leaf have mucilaginous inner walls (see also KRUCH). In the leaves investigated the palisade parenchyma consisted of 2—3 layers of cells. The thickness of the leaf varied between 132 μ (N. E. Greenland) and 192 μ (Norway) and the proportion between the leaf-thickness and the thickness of the palisade parenchyma was $\frac{2}{1}$. In the two upper layers of the palisade parenchyma the cells were well-formed; they inclosed large intercellular spaces. The spongy parenchyma was loose in structure and consisted of slightly branching cells (Fig. 10, *E*). Here reference should be made to BONNIER (l. c.) who in leaves from Spitzbergen found two layers of palisade-cells which were scarcely longer than they were broad. In specimens from the Alps he found 3—5 layers of palisade-tissue: the cells were narrow and well-formed, and intercellular spaces were either wanting or few in number.

WARMING says in his notes regarding the flowers from Greenland: "The flowers are highly conspicuous on account

of the intensely yellow petals which are either of one colour or have an orange-coloured spot at the base. Honey is secreted abundantly." According to WOLF the diameter of the flower is 10—15 to 18 mm. The flowers in my material from northern Norway and from Greenland were homogamous, and appeared to behave like those of *P. emarginata.* The five innermost stamens which stand before the sepals are longer than the others and rise upwards almost to the level of the pistils. In flowers from Kongsvold and Alten in Norway it could be seen how the somewhat outwardly bent styles touched with their stigmas the open anthers of these stamens. WARMING (l. c.) also finds that the anthers and stigmas are developed simultaneously "and the stamens stand so erect and close to the pistils that self-pollination must undoubtedly easily take place (Fig. 11, *A*)." In Scoresby Sound HARTZ (l. c. 1895 a) observed *Syrphids* to visit the flowers of *P. nivea.*

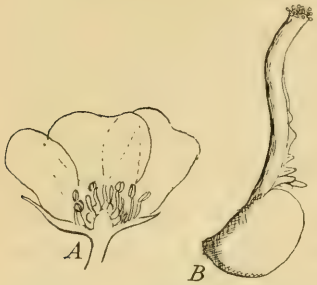

Fig. 11. *Potentilla nivea.* *A*, Longitudinal section through a flower from Spitzbergen (about $^2/_1$). Drawn by Eug. Warming. *B*, Carpel showing the peg-shaped cells at the base of the style (about $^{24}/_1$).

NORMAN records that the flowering period is in the latter half of July and in the first half of August; CLEVE: from June 30th to July 10th; LANGE: July—August in Greenland where HARTZ, however, in 1889, 1890 and 1892 found it flowering in the middle of June. In tke botanical museum of Copenhagen there are flowering specimens from different places in N. Greenland gathered at the end of June.

P. nivea sets fruit abundantly probably everywhere. Fruit-dispersal is as in *P. emarginata.* Greenland specimens gathered on the 4th of February on ground free from snow had ripe fruit enclosed between the contracted sepals, and WARMING (notes) found (July 15) fruit from the preceding year hidden in the same manner.

Potentilla Vahliana Lehm.

Lit. Simmons, 1906. Wolf, 1908.

This is an Arctic species which lives in North-West Greenland, Arctic America and adjacent islands (Unalaschka) and perhaps the Rocky Mountains. It occurs in dry localities exposed to the sun, especially when they are gravelly, and extends to the snow-line (Wolf, Lange). The alcohol material was collected near Godhavn on Disco.

Pot. Vahliana is a plant with a tufted growth: it has a strong, long, multicipital primary root. An almost unbranched primary root on a small tuft from Godhavn, which Warming had measured, was 60 cm. long. The numerous shoots are covered, almost for their whole length, with dead leaves and remains of leaves, pressed closely together, and upon the surface of the tuft the living leaves hardly protrude above the old dead ones (Fig. 12, *A*). Adventitious roots, which may be fairly vigorous, may arise from the shoots, but vegetative propagation is undoubtedly only a rare occurrence. The shoot-structure is monopodial. The lateral flowering stems bear 1—2 small leaves and 1—2 large flowers. The whole plant is covered with long, yellow hairs.

Fig. 12. *Potentilla Vahliana* (Godhavn on Disco, July 7).

A. A shoot-complex about 10 years old; about 1/2. Above are seen two flowering stems and one which has finished flowering protruding from among the living leaves; for the rest, the greater part of the shoots are covered with dead masses of leaves, through which the remains of the flowering stems of previous years are protruding. B, Leaf; about 1/2. Drawn by Eug. Warming.

Anatomy. I have not examined the roots.

The structure of the rhizome agrees in its chief points with that of *Pot. pulchella*. The pith is however considerably smaller; the greater part of it was found to be compressed; it contained starch, as did the other

depository tissues of the rhizome, and, in addition, large sphaero-crystals. The shoot may attain a considerable age. In the oldest part of the shoot in my material about 15 partially indistinct annual rings could be counted with an average breadth of about 40 μ. Even at this age the rhizome is closely covered with dead fragments of leaves. An endodermis is present.

In the flowering stem there is no distinct endodermis. Outside the vascular bundles, about 10 in number and separated by broad medullary rays, there is a ring of stereom consisting of 3—7 layers of slightly lignified bast. The outer part of the medullary rays also becomes woody. The structure of the cortex is similar to that of *Pot. pulchella*. The epidermis consists of rather small cells; the tangential walls are about 6.5 μ thick. The pith is homogeneous.

The leaf is hairy on both surfaces, but more so upon the lower (Fig. 13, *A*), where there also occurs a fair number of glandular hairs of the type figured (Fig. 13, *E*); the stalk is 2—4 celled. Besides in the alcohol material, fairly large numbers of glandular hairs are shown also on leaves from Ellesmereland (determ. SIMMONS) and from King Point in Arctic America (determ. OSTENFELD), contained in the herbarium of the Botanical Museum in Copenhagen; (see *Pot. nivea* p. 31). The glandular hairs may also occur upon the upper surface of the leaf along the margin.

The outer wall of the upper epidermis is about 2.5 μ thick; the inner wall is not mucilaginous. The radial walls of the upper epidermis are almost straight (Fig. 13, *C*), of the lower undulating. Stomata occur only upon the lower surface, and as seen in the figure, they often project somewhat, a fact which should doubtless be correlated with the dense hairy covering (compare *Pot. pulchella* and *Pot. nivea*). There are two layers of coarse palisade-cells and a rather loose spongy parenchyma the cells of which are slightly

branched (Fig. 13, *B*, *D*). The thickness of the leaf was about 140 μ and the proportion between the leaf-thickness and the thickness of the palisade parenchyma was $\frac{2}{1}$. Some weak bast occurs upon the under side of the main bundle of the leaf and also at the leaf-margin when a bundle runs along the latter.

The diameter of the flower is somewhat large, Wolf records 18—20 mm.; the petals are broader than long and yellow in colour, and these large, conspicuous bowls doubtless

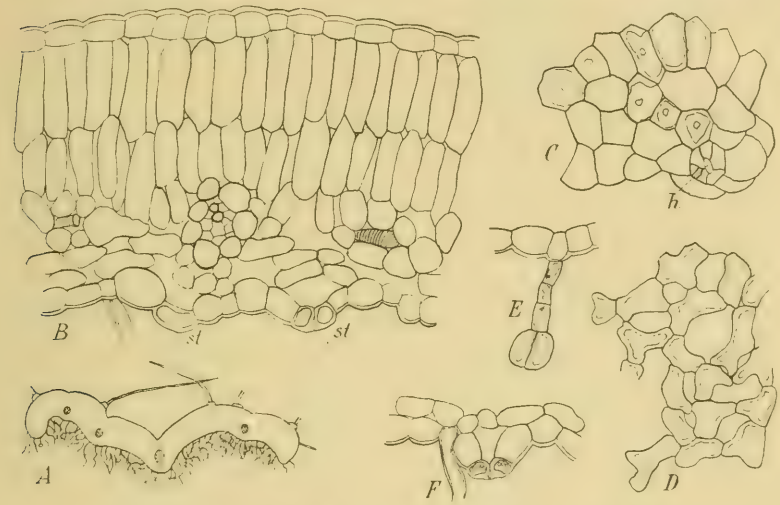

Fig. 13. *Potentilla Vahliana* (Godhavn on Disco).

A, Transverse section of a leaf-lobe, the edges are revolute, the lower surface is tomentose. *B*, Transverse section of leaf; *st*., stoma. *C*, Epidermis of the upper surface; *h*, cross section of a hair which is standing on a small stalk. *D*, Section of spongy parenchyma parallel to the surface. *E*, Glandular hair from the lower surface of the leaf. *F*, A highly projecting stoma which was found behind the revolute leaf-edge. (*A*, about $^{25}/_{1}$; *B*, *C*, *D*, *E* and *F* $^{215}/_{1}$).

readily attract insects. Warming states in his notes that honey is secreted abundantly. According to Warming's notes, of the 20 stamens the episepalous are longer than the epipetalous and stand more erect against the pistils. To judge from my alcohol material *Pot. Vahliana* appears to be homogamous, and self-pollination probably takes place.

Flowering begins in July; according to Simmons it lasts only a short time. Fruit is set abundantly (Simmons).

Potentilla emarginata Pursh.

Lit. ABROMEIT, 1899. HARTZ, 1894, p. 32; 1895 a., p. 288; 1895 b., p. 322. EKSTAM, 1897. SIMMONS, 1906. WOLF, 1908.

This plant is high northern and circumpolar. In Greenland it lives on rocky and grassy flats; on Nova Zembla it prefers dry slopes exposed to the sun (EKSTAM).[1]

The alcohol material was collected in Greenland in different places.

Pot. emarginata has a strong, multicipital primary root which may attain a length of at least 25 cm. and a thickness of 6 mm. During the first years the seedling is in the form of a rosette without lateral shoots; the specimen figured has just entered on its second- or perhaps its third summer (Fig. 14, *A*). Later on it branches freely and very compact tufts rich in shoots, measuring as much as 20 cm. in diameter, may be formed. Looser tufts are however often found; these plants have probably lived in more favourable localities. The shoots in such tufts are ascending or may at first have a horizontal part several cm. in length. Often adventitious roots, which may even be somewhat vigorous, arise from older shoots, though this is hardly a normal occurrence, and then vegetative propagation may take place or, rarely, even a slight vegetative wandering may occur. The large brown sheaths of the spirally arranged leaves persist for several years, but the shoots may ultimately get rid of them.

The floral shoots are lateral. They usually bear 1—2 leaves and are ascending or the lower portion is prostrate. They are subtended by those leaves which in the autumn occur uppermost in the rosette upon the monopodial main

[1] EKSTAM (l. c.) records *P. fragiformis* Willd. from Nova Zembla, but as this species, according to WOLF, does not occur on Nova Zembla, he has probably had specimens of *P. emarginata* before him, as these two species are commonly confused (cf. WOLF, p. 510).

shoot. Plants from Kekertak in Greenland collected Sept. 14 had formed flower-buds for the next summer, which had developed so far that the exterior of the stamens was fully formed and in the interior the mother-cells of the pollen-grains could be seen; the carpels were formed, but no indication of the formation of ovules could be observed. In the specimens from Upernivik (May 17) the young flowers were somewhat larger; as yet no pollen was to be seen, but in the carpels the style was formed, and in the ovules the embryo-sac could be seen.

The plants probably pass the winter with dead leaves; in Kekertak they had withered in the middle of September 1886, and in Upernivik they began to unfold in the beginning of June 1887. The shoot-apices are protected by the leaf-sheaths; scale-leaves are not developed.

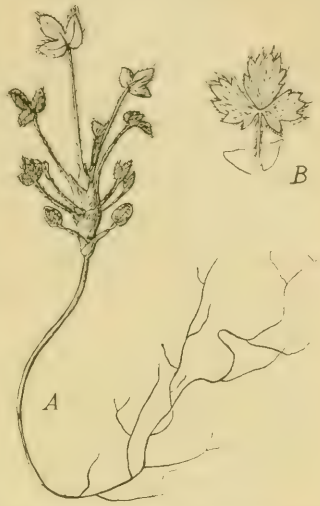

Fig. 14. *Potentilla emarginata.*

A, Seedling from Lille Snenæs in N. E. Greenland (25. 6. 1908; about $^2/_5$); the cotyledons and the lower darkly shaded leaves were dead and date probably from 1906 and 1907; there are two fresh leaves at the shoot apex; the primordial leaves have a simpler form than the leaves of the full-grown plant. *B*, Leaf of a full-grown plant from Spitzbergen; somewhat reduced. (Drawn by Eug. Warming.)

Anatomy. The structure of the slender absorbent roots is shown in Fig. 15, *F*. The epidermis is very weak and collapses, on the other hand the structure of the exodermis is very strong especially in its radial walls. The rest of the cortex consists of a few layers of cells in which balls of fungal hyphæ occur; in the intercellular spaces fairly vigorous hyphæ are found. In the secondary woody portion, which begins to develop early, the medullary rays are absent from the slender roots, but in the older roots broad, non-

lignified medullary rays are gradually formed, similar to those which are found in the primary root, of which they may constitute the main portion. The rays of wood contain much parenchyma. The periderm consists of alternating layers of cork-cells and phelloid-cells; in the former the walls of the lateral roots are specially strong. The intercellular spaces are fairly large in the periderm; they are absent from the inner side of the cork-layers. The outer part of the secondary cortex becomes gradually compressed owing to growth in thickness. The primary root which, as already mentioned, may attain a thickness of at least 6 mm. is doubtless the chief depository of food-material.

The rhizome is similar in structure to that of *Pot. pulchella*. In the periderm 1—2 layers of phelloid-cells alternate with a layer of cork-cells. The intercellular spaces are rather large; they are absent from the inner side of the cork-layers. The rhizome may attain an age of at least about 15 years.

The material at my disposal allowed an investigation of the amount of the food-materials — starch and fat — contained in the rhizome in the months of May, June, July and September, with the following result:—

	17. V	4. VI	medio. VII	14. IX
Starch.	a little	rather much	much	much
Fat.	much	rather much	a little	a little

(Cf. *Pot. nivea*). Though the rhizomes investigated were collected in different localities and in different years yet the investigation is of some interest particularly as regards this plant which is hardly green during winter. Plants from the second column were collected on June 4, and the leaves were not unfolded; consequently, the very decided increase in the amount of the starch as compared with the plants in the first column cannot be due to new acquisition, but must have been produced by the transformation of other materials which

were already present. The simultaneous decrease of the amount of the fat may indicate that some of this material has been used in the starch-formation, though naturally nothing can be stated with certainty on this basis. Besides, there are other materials than fat in herbaceous plants which, like the latter, decrease in quantity during spring.[1]

The vascular bundles in the floral shoot vary greatly in number (7—17) and are surrounded by a sheath of several-layered stereom which is well-developed especially opposite the vascular bundles; the outer part of the woody portion of these bundles is connected with the bast-sheath, so that the groups of sieve-tissue are surrounded by stereom. The cortex is similar to that in *Pot. pulchella*. The outer wall of the epidermis is about 5 μ in thickness. The inner portion of the pith breaks down. An endodermis is not present.

The leaf of *Pot. emarginata* is most nearly mesophilous; the thickness is about 170 μ. Along the margin and along the bundles of the leaf a fair number of long hairs occur; upon the surface of the blades these hairs are fewer, but short-stalked glands are rather numerous especially upon the lower surface (Fig. 15, *A B*), a fact which has also been observed by Abromeit (l. c.). The outer walls of both upper and lower epidermis are about 2 μ in thickness; the inner walls of the upper epidermis are not mucilaginous. As regards the radial walls of the upper and lower epidermis the reader is referred to figure 15, *C* and *D*. Stomata occur on both surfaces, but they are more numerous upon the lower surface where they may project slightly; upon the upper side they are on a level with the surface. The coarse, somewhat barrel-shaped palisade-cells occur in 2—3 layers. The proportion between the leaf-thickness and the thickness of the palisade parenchyma is found varying from $\frac{2}{1}$ to $\frac{2.5}{1}$.

[1] Ernst Michel, Zur Kenntniss der Jahresperiode unserer Stauden. Inaug. Dissertat. Göttingen, 1909.

The spongy parenchyma consists of shortly branched cells and has a loose structure (Fig. 15, *A*, *E*). Slit-like lacunæ are often found upon the dorsal side of the leaf. Stereom is absent.

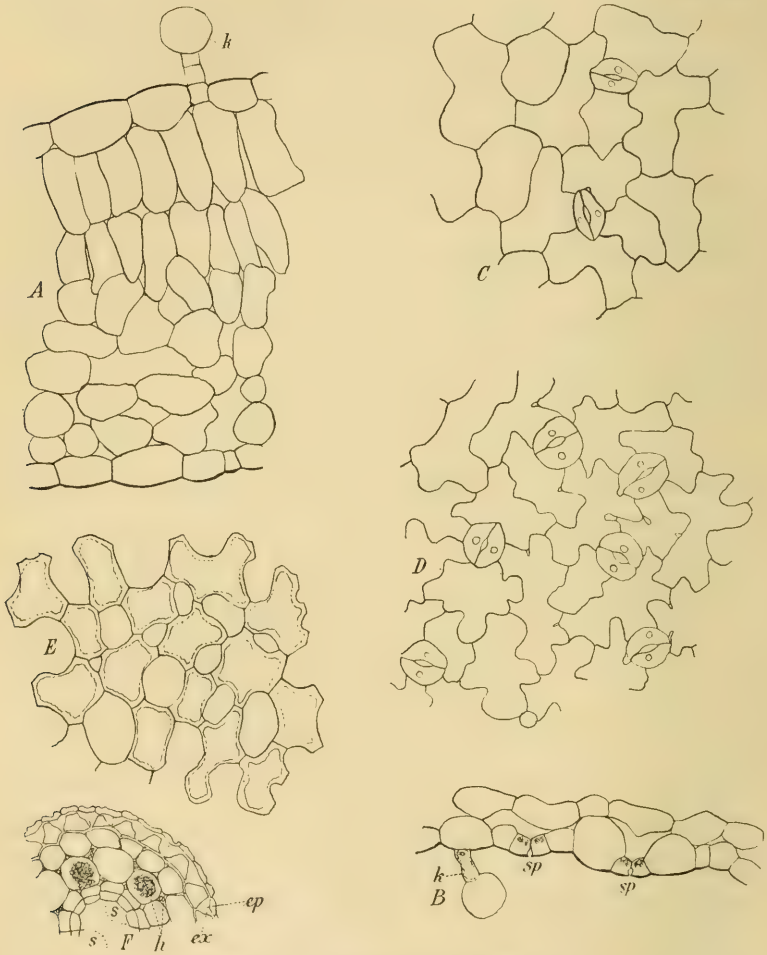

Fig. 15. *Potentilla emarginata.*

A, Fragment of a transverse section of a leaf; *k*, a glandular hair. *B*, Epidermis from the lower leaf-surface with 2 stomata and a glandular hair *k*. *C* Epidermis of the upper leaf-surface. *D*, Epidermis of the lower leaf-surface. *E*, Section of the spongy parenchyma of the leaf. *F*, Transverse section of an absorbent root; *ep*, the collapsed epidermis; *ex*, exodermis; *h*, fungal hyphæ, which partly forms balls in the cortical cells and partly fills out the intercellular spaces; *s*, the leptome-groups of the central cylinder. *A*, From Lille Snenæs; *B*, *C*, *D*, *E* and *F* from Upernivik (*A*, *B*, *C*, *D*, *E* and *F* about $^{220}/_{1}$).

According to Lange the flowering period in Greenland is in July—August, and on Nova Zembla the plant flowers in the middle of summer and late in autumn (Ekstam)[1]; but Hartz found it in flower on Præstefjæld in Greenland on June 15, and at Scoresby Sound on June 19; in Ellesmereland the flowering begins in the middle of June and is continued into August (Simmons). In my alcohol material there were numerous flowers from Upernivik gathered on June 21. *Pot. fragiformis* Willd. *f. parviflora* Trautw., which is perhaps a synonym of *Pot. emarginata* (cf. Wolf, p. 533), according to Andersson and Hesselman (l. c.), is a spring plant in Spitzbergen; it flowers in the middle of June and in the beginning of July. *Pot. emarginata* sets fruit abundantly (Ekstam, Simmons).

The large, pale yellow flowers occur either singly or 2—3 together on the floral shoot. Wolf states the diameter to be 15—18 (—20) mm., Ekstam records 20 mm. from Nova Zembla, while *Pot. fragiformis f. parviflora* from Spitzbergen has flowers only 10—14 mm. broad (A. and H.). Ekstam found no scent, but he found honey which is secreted between the stamens and on the base of the filaments. He was of opinion that homogamy and self-pollination were possible as the stamens were bending over the stigmas. Of the stamens the 5 innermost are the longest and in the spirit-material they were only very slightly separated from the stigmas. Warming writes in his notes regarding specimens from Spitzbergen that these 5 antesepalous stamens which he also found to be the longest, are without doubt easily able to shed pollen upon the stigmas. They open later than do the others. I also find that *Pot. emarginata* is homogamous (Upernivik and Lille Snenæs), perhaps with a short proterogynous stage. In case pollination fails for some reason or other, the 5 innermost

[1] See note, p. 36.

and longest stamens remain as a reserve which ensures self-pollination (Fig. 16).

Of a large collection of flowers preserved in spirit and gathered at Upernivik on June 21, 1887, a great number were found with more or less abortive stamens. All transitions from normal to purely female flowers were found. The abortive stamens were shorter than the head of pistils and the anthers were small and shrunken, even in quite young flowers; they contained no pollen. The carpels were apparently normal though the styles were somewhat short, but no pollen was found on the stigmas which were furnished with large papillæ, and no fertilization had taken place in the older flowers.

Fig. 16. *Potentilla emarginata.*
A, Longitudinal section through a flower; $^4/_1$. *B*, Pistil with hairs at the base; stigma with many small conical protuberances; $^{18}/_1$. Spitzbergen. (Drawn by Eug. Warming.)

According to EKSTAM on Nova Zembla "*Pot. fragiformis Willd.*" is visited by flies and other diptera.

As is usual in the *Potentillas* the calyx is persistent and closes around the fruits, whereby their dispersal is regulated. The fruit-dispersal is anemophilous (EKSTAM).

P. maculata E. M. vix Pour.

Syn. *Potentilla alpestris* Hall f.

Lit. HARTZ, 1894, p. 4; 1895 a., p. 288. NORMAN, 1895. ABROMEIT, 1899. ANDERSSON and HESSELMAN, 1900. CLEVE, 1901. SYLVÉN, 1906. WOLF, 1908.

The alcohol material is from Spitzbergen and Greenland

Wolf is of opinion that, judging from its present distribution, this plant is an old species which was probably originally circumpolar and has only recently advanced southwards to about 40° N. lat. In Arctic and Subarctic regions it is found both in the mountains and near the sea, in southern regions (Europe and western Asia) only in Alpine and Subalpine mountain regions.

It grows on rocks, on heaths on grassy slopes and in copses.

The shoot-structure is monopodial and caespitose, but the tuft is rather loose in form, and ascending or almost horizontal branches, 10—15 cm. in length, commonly occur. There is some individualization of the older branches. The branches are for many years covered with the remains of brown leaf-sheaths.

Sylvén writes that in Sweden *Pot. maculata* is evergreen even in mountainous regions and in the Copenhagen herbarium there are specimens with green leaves from Disco in Greenland gathered in September and in the beginning of April. In a garden in Copenhagen it remains green through the winter.

Anatomy. My material of *Pot. maculata* was extremely poor with regard to roots; but it appeared that the exodermis of the absorbent roots has thin walls very much as in *Pot. Anserina*. The epidermis of the absorbent roots proved to have collapsed. No mycorrhiza was seen.

The structure of the rhizome resembles in its main points that of *Pot. pulchella* (see Fig. 9, *G*), the medullary rays are however fewer in number—about 4. Fairly distinct annual rings were seen in the wood. A shoot, 7 cm. long, was about 6 years old, and another which measured about 3 cm. was of the same age. The pith in these shoots was still alive. The secondary cortex had somewhat thickened walls and its outermost part was found to be somewhat compressed. The periderm is thick, there are about 6 layers of

cork each separated from the other by a layer of phelloid. In this species also, intercellular spaces are absent from the inner side of the cork-layers.

Fig. 17 shows a portion of the transverse section of a floral shoot which may serve as an example of the stem-structure of the monopodial *Potentillas* mentioned in the present work. The vascular bundles may vary somewhat in number in the different species. The primary groups of vessels always remain distinct: the function of the cambium is slight. The pericycle is transformed into a rather strong bast-ring, about 3—6 layers thick. No distinct endodermis is present. The structure of the cortex is similar to that described for *Pot. pulchella.*

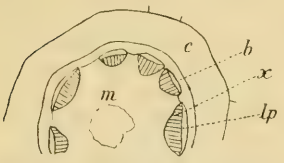

Fig. 17. *Potentilla maculata.* Portion of a transverse section of a floral shoot (about $^{17}/_{1}$); *b*, bast; *c*, cortex; *lp*, leptome; *m*, pith, in its centre the cells are somewhat disorganized; *x*, xylem.

The leaves are almost glabrous or slightly hairy upon the upper surface, and upon the lower surface the hairs are sparsely scattered. The hairs are projecting. LANGE maintains that *Pot. Frieseana* Lge. is distinguished from *Pot. maculata* Pour. among other things by the fact of the leaves being glandular, but ABROMEIT states that in Sweden he has found numerous yellow glands upon the lower surface of the leaves of the latter species. In the key given by WOLF of the determination of the forms of *Pot. maculata*, among the northern forms leaf-glands are assigned only to *Pot. Frieseana* (found only on Disco). I have, however, usually found numerous short-stalked glands on both leaf-surfaces of *Pot. maculata* from the majority of the localities represented in the Arctic herbarium in Copenhagen. The glandular hairs occur in unequal quantities in different plants and on the different leaves of the same plant; upon the upper surface they often occur especially in the furrows above the larger bundles. The form of the glands is shown in Fig. 18, *D.*

The outer wall of the epidermis of both leaf-surfaces was 3—4 μ thick. In the epidermis of the upper surface a mucilaginous inner wall was found in a great many of the cells, and in specimens from a single locality in Greenland (Kangerdlugsuatsiak) a few cells in the lower epidermis had also mucilaginous inner walls. Such cells were often larger than the other cortical cells (Fig. 18, *A*, *B*, *C*; cf. p. 57). The stomata are far more numerous upon the lower than upon the upper surface; they are situated on a level with the surface.

The palisade parenchyma consist of 2—3 layers of cells and contains large intercellular spaces. The spongy parenchyma is often composed of short, stellately branched cells and is more or less loose in structure. In the subepidermal layer of the present species more branched cells occur than in the other *Potentillas* mentioned in this work.

As may be seen in the two figures of the transverse section of the leaf, this varies considerably in thickness, from 160 μ to 240 μ. In the thick leaf from Spitzbergen Fig. 18, *A*, which was somewhat fleshy and almost smooth there were three layers of well-marked palisade-cells, and the proportion between the leaf-thickness and the thickness of the palisade parenchyma was about $\frac{2.1}{1}$. The spongy parenchyma was specially loose in structure owing to its large intercellular spaces. In Fig. 18, *B* are shown 2 layers of less well-marked palisade-cells and the proportion mentioned above was in this leaf about $\frac{2.9}{1}$; here the spongy parenchyma was somewhat more compact. Unfortunately nothing is known with regard to the conditions in which the different plants were living. It is however of some interest that this difference in the leaf-structure in a single species is also found, though in a more marked degree, in other Arctic plants, viz. among the land-species of *Ranunculus*. The thin leaf of *Pot. maculata* (Fig. 18, *B*) resembles in the structure of the mesophyll the type

exhibited by the majority of the land-species of *Ranunculus*, while a further development in the direction indicated in Fig. 18, *A* would lead to a leaf of the *R. glacialis* type[1].

The diameter of the flower varies greatly; WOLF records

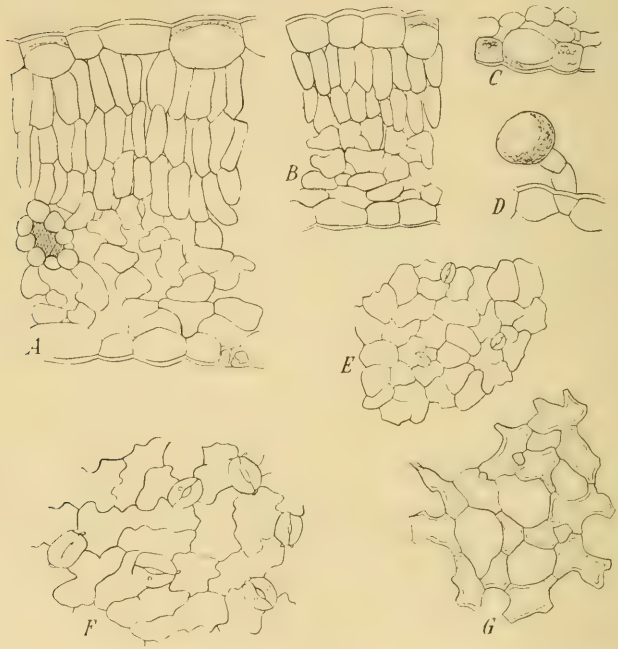

Fig. 18. *Potentilla. maculata.*

A, Transverse section of leaf. *B*, Transverse section of leaf. *C*, Cortical cell with mucilaginous inner wall from the lower surface of the leaf. *D*, Stalked gland from the upper leaf-surface. *E*, Epidermis of the upper leaf-surface. *F*, Epidermis of the lower leaf-surface. *G*, Section of the outermost layer of the spongy parenchyma. *A* and *G* are of leaves from Spitzbergen, the others are of leaves from Greenland (*A*, *B* *C*, *D*, *F* and *G* about $^{175}/_{1}$; *E*, about $^{60}/_{1}$).

from 10 to 25 mm. I measured flowers from Greenland which were about 15 mm. in diameter. The petals are usually golden yellow in colour, sometimes they are of one colour, sometimes there is a saffron coloured spot at the base (WOLF).

[1] *Ranunculaceæ* by KNUD JESSEN: Arctic Flow. Pl. I. 6. Meddel. om Grönland, Bd. 36.

The flowering period is June-September. Flowers from Bosekop (Arct. Norway) were found to be distinctly proterandrous; the next stage is homogamous, and it is probable that self-pollination takes place in the latter, as the outermost of the somewhat outwardly directed stigmas are either in direct contact with the inner erect or slightly inwardly bent anthers, or they are only slightly separated from these inner anthers which occur either at the same level as the stigmas or at a somewhat higher one. *Herman Müller* investigated a *Pot. verna* L[1] in the Alps in which he found the anthers developed simultaneously with the stigmas. He writes that as the flowers in inclement weather remain half-closed and during the night entirely closed, self-pollination is ensured if cross-pollination fails.

The fruit does not ripen in the mountains of northern Sweden (Cleve).

Potentilla anserina L.

Lit. Warming, 1884. Knuth, 1894. Norman, 1895. Coville, 1896. Porsild, 1902. Poppius, 1903. Sylvén, 1906. Wolf, 1908.

As regards the distribution of this species in Arctic Norway Norman writes that the strand and the fore-shore were most likely its original habitats and as the result of civilization it has been brought inland where it occurs especially along road-sides and near houses. This supposition is no doubt true for other regions also; thus Coville (l. c.) records that in Yakutat-bay in Alaska where *Pot. anserina* is common it is confined to the beaches. On Disco Porsild found var. *Egedii* in such places only, where it would be washed by the sea. Both Norman and Wolf think that *P. anserina* is dispersed by the agency of the sea, and the latter author writes that the fruit or even whole shoots ("ganze Stöcke")

[1] It is uncertain whether this was a *P. maculata* or a *P. minor* Gil.

can withstand being carried a long distance in salt water without getting damaged. Fig. 21, *F* shows a transverse section through a ripe fruit. In the wall, within a few layers of cells which keep alive a long time, there occurs a considerable area of dead cells containing air. The shaded part is sclerenchymatous. I have found no difference in the degree of development of this floating tissue in the fruit of var. *Egedii* which PORSILD gathered on the strand on Disco and in the fruit of a specimen of the typical form which had been growing in Denmark at a distance from the sea.

Pot. anserina is almost cosmopolitan; for further notes regarding its distribution the reader is referred to WOLF.

The alcohol material is from Greenland and Denmark.

SYLVÉN has observed the germination during spring in nature. During the second year the slightly branched primary root was found to be about 3 mm. thick and spindle-shaped; sometimes, however, it is rather weak and then an adventitious root takes on its function. In older plants the primary root is absent.

The short, vertical rhizome is monopodial and the annual growth-increment hardly lives more than one year; the leaves die away every autumn and the shoot-apices are protected by scale-leaves. The rosette-leaves subtend from one to several runners, which may attain a length of about one metre; but the longest runner I have seen from Greenland was only about ½ metre long. According to WARMING, who mentions *Pot. anserina* in his paper of 1884, these sympodial runners are to be compared with the lateral floral-shoots in *Pot. erecta* (L.) Dalla Torre. The single shoot-generations consist normally of a long and a quite short internode, after which they terminate in a flower. At the base of the flower-stalk are two small connate bracts of which the lower subtends an assimilatory shoot which has leaves in a rosette and as a rule soon produces 1—2 strong adven-

titious roots, while the upper bract subtends a new runner of the same appearance as the parent-shoot. "The leaf-shoots lie alternately to the right and left on the runner-sympodium, from which it is evident that the branching is as in a true scorpioid cyme" (Warming l. c.). From the new adventive plants new runners may arise even during the first summer (Wolf).

As every runner may produce several new rosettes, when circumstances are favourable, a parent-rosette of this plant may give rise to a considerable number of new individuals all around it. The runners die during autumn and by this means the young shoots become independent. On the other hand, in less favourable localities, where the runners are short, the number of off-shoots is considerably reduced, and it is especially those shoots which are nearest to the parent-plant which succeed in striking root and becoming independent. It appears, especially in dry soil, to be a critical moment for the young shoot when its roots emerge, because these easily get dried up before they succeed in penetrating deep enough into the soil. Further, it is only the inner shoots or only the innermost one of the shoot-generations of the runners which attain the flowering stage in unfavourable localities. In cases where the flower is not immediately visible, an extremely small dead flower-bud may often be found hidden among the bracts.

Besides these creeping floral shoots the leaves of the parent-rosette may also subtend new rosette-shoots which may sooner or later become independent.

As already mentioned the young adventive shoots are provided with 1—2 strong adventitious roots. The latter die in the course of the following summer while new ones are developed. In older plants these one-year-old roots often take the character of a food-storing root as shown in Fig. 19. They are usually spindle- or club-shaped and may become

about 8 mm. thick and about 10 cm. long; they do not branch, but bear thin absorbent roots. During winter they are found crowded with starch which appears to be transformed to fat only in a very slight degree.

Pot. anserina, like many other plants, has the power of keeping its growing point on a level with the surface of the ground, at any rate if the shoot-apex has been covered with a layer of earth and in such a case the fresh food-storing roots are in the autumn often found to be raised as much as 2 cm. above the remains of the shoot-base of the previous year upon a portion of the axis with elongated internodes.

Fig. 19. *Potentilla anserina* (Denmark; 28. 9. 1912.).

Autumn stage; the runners dead or dying; *l*, the leaf-bases; *d*, the dead food-storing root of 1911—12; *f*, two fresh food-storing roots which have been developed in the summer of 1912 (somewhat reduced).

Anatomy. In the slender absorbent roots of the first and second order considerable quantities of strong fungal hyphæ occur which form balls in the cells of the loosely built cortex. The epidermis, especially of the absorbent roots of the second order, is very small-celled, very much as in *Potentilla palustris*, but the outer wall is thinner, and the skin is collapsed; nor are the dark contents found in *Pot. palustris* present here.

Fig. 20, *A* shows the structure of the fully developed food-storing root. On the outside is seen the thin cork with a few fragments of the primary cortex, then follows the thick secondary cortex and lastly a few groups of vessels around the small pith. Not until during the beginning of summer is a continuous woody part developed in the middle

of the root. The secondary cortex consists chiefly of parenchyma. It shows concentric layers which result from circles of sieve-tube-groups, the cambium for each circle of such groups producing about 10 layers of parenchyma. Fig. 20, *B* shows a group of sieve-tubes just outside the cambium, while Fig. 20, *C* illustrates two such tubes from about the middle of the cortex.

In the rhizome, as in the food-storing root, a continuous cambium develops chiefly parenchyma. The periderm in correlation with the short duration of life is not very thick. An endodermis is present.

The horizontal portions of the floral shoots are somewhat flattened. The activity of the cambium is slight, and the few groups of vessels always remain separated by primary medullary rays. The two-layered pericycle is transformed to bast which becomes somewhat stronger in the peduncle than in the horizontal part. An endodermis-like layer is present[1]. Within the epidermis there is a layer of weak collenchyma. The stomata project above the level of the surface.

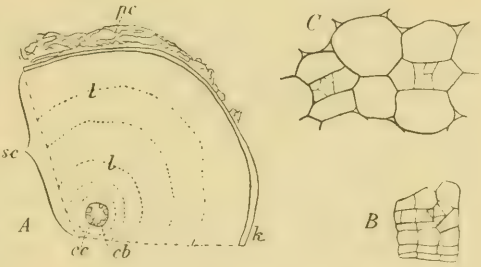

Fig. 20. *Potentilla anserina.*

A, Fragment of a transverse section of a food-storing root taken in the autumn ($^{16}/_{1}$); *cc*, central cylinder with groups of vessels; *cb*, cambium; *sc*, secondary cortex; *pc*, fragments of the dead primary cortex; *k*, cork; *l*, concentric circles in the secondary cortex with groups of sieve-tubes. *B*, A group of sieve-tubes just outside the cambium. *C*, Groups of sieve-tubes from about the middle of the secondary cortex. *B*, *C* about $^{210}/_{1}$.

The leaf varies considerably in size being from about one-third of a metre (*f. grandis* Lehm.) to 3—4 cm. in length, the hair-covering is also very different; in *f. sericea* Hayne,

[1] Cf. Edmund Orth: Beitr. z. Anatomie d. Gattung. *Potentilla.* Dissert. Hamburg. 1893, p. 27.

which occurs especially in dry localities, both surfaces of the leaf are white with silky hairs, in the typical form this is the case only on the lower surface, and in the Arctic and Subarctic var. *Egedii* Torr. and Gr. and var. *gronlandica* Tratt. the leaves are entirely glabrous or somewhat hairy, on the lower surface only, respectively. Fig. 21, *D* shows a stalked

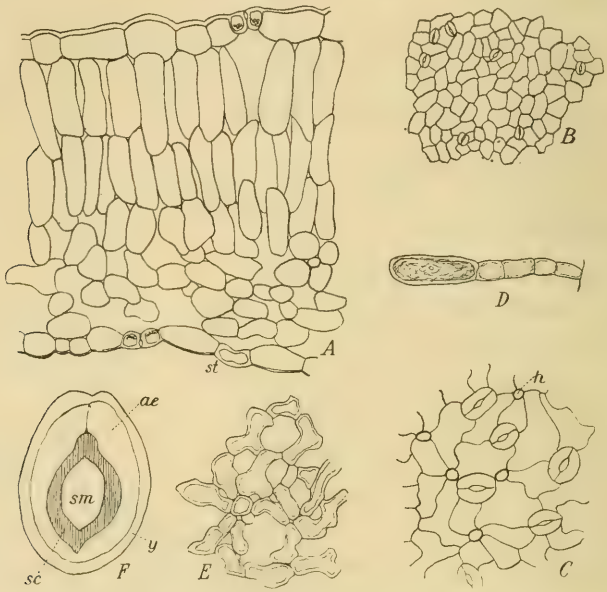

Fig. 21. *Potentilla anserina* (Greenland).

A, Transverse section of leaf. *B*, Surface view of the upper epidermis of the leaf. *C*, Surface view of the lower epidermis of the leaf; *h*, a hair-bearing cell. *D*, Stalked gland from the lower surface of the leaf. E, Surface view of spongy parenchyma. *F*, Transverse section of an almost ripe pistil; *sm*, the seed cavity; *y*, outer layer of the fruit-wall; *ae*, floating tissue; *sc*, sclerenchyma (*A*, *C*, *D*, *E* about $^{185}/_{1}$; *B* about $^{65}/_{1}$; *F* about $^{15}/_{1}$).

gland; such occur scattered along the bundles and are more common on the lower surface.

The anatomical structure of the leaf, which only lives through one summer, is mesomorphic. The outer wall in the epidermis of the upper surface is about 2.5 μ thick; the radial walls are straight or almost straight (Fig. 21, *B*), but in that of the lower surface somewhat undulating (Fig. 21, *C*).

The palisade parenchyma consists of 2—3 layers of cells, of which the two upper layers are fairly well-marked. The proportion between the thickness of the leaves from Greenland and the thickness of the palisade parenchyma is about $\frac{1.7}{1}$. The spongy parenchyma is rather loose and consists of slightly branching cells (Fig. 21, *A*, *E*).

It is normal for the yellow flowers to occur singly on the often long flower-stalks. Wolf records the diameter of the flower as 18—20 mm., and Knuth as 20 mm.

The flowering period occurs in Arctic Norway between June 25 and Sept. 21 (Norman), Lange records as regards Greenland July—August; in Central Europe the flowering begins in May.

My material contained flowers from different localities in Greenland, and those which had not entered the homogamous stage showed a somewhat considerable degree of proterogyny. Anthers in fully expanded young flowers were still closed while the stigmas were found to be highly papillose even before the petals had opened. It was, however, impossible to find a single pollen-grain on these highly papillose stigmas, but, as soon as the anthers had opened the stigmas were found to be densely covered with pollen. This fact does not seem to indicate that insect-invisitors have been frequent. The stamens are longer than the styles; they are erect or somewhat bent inwards when the anthers are open. Self-pollination is consequently possible, which opinion is also maintained by Knuth. In the Friesian Islands he found *Pot. anserina* to be purely homogamous, and he writes that spontaneous self-pollination must take place as soon as the pollen-grains no longer adhere to the drying pollen-sac; he found that there was a possibility for insect-pollination in the fact that at first the pollen was rather firmly attached to the open pollen sacs. According to Knuth in inclement weather the flowers are half-closed during the day and entirely

closed at night, and this makes self-pollination possible. POPPIUS found the flowers to be slightly protandrous at Esbo in Finland; they were very sparsely visited by insects.

Concerning the fruits see p. 48.

Sibbaldia procumbens L.

Lit. WARMING, 1886, *a.* LINDMAN, 1887. HARTZ, 1895, *a.* NORMAN, 1895. A. CLEVE, 1901. KJELLMAN, 1901. SYLVÉN, 1906. HOLLSTEIN, 1907.

This species grows in grassy and often somewhat damp localities, not, however, in bogs (CLEVE). It is circumpolar, and occurs also in Great Britain, Iceland, the Færöes and the Alps.

The alcohol material was collected in Spitzbergen and in Greenland, in different places.

According to SYLVÉN the seedling has a slender, slightly branched main root which together with the hypocotyl quickly becomes woody. From the leaf-axils of the first young rosette monopodial lateral shoots are developed sooner or later, which in the course of time may attain a considerable length; they become prostrate and have a somewhat upwardly turned apex. The primary root may live for a long time, and in the museum of the Botanic Garden in Copenhagen tufts are found, 20—30 cm. in diameter, the numerous, closely placed shoots of which are still in connection with the vigorous main root. KJELLMAN (l. c.) writes that *Sibbaldia* either does not develop adventitious roots or does so only very slightly; but this statement does not quite agree with the specimens I have seen in the herbarium mentioned above; to judge from the latter, adventitious roots — even vigorous ones — may be fairly often developed from older branches, and the plant is certainly not dependent on its primary root, but has some power of vegetative propagation. The shoots are

more or less covered by the dead shoot- and leaf-masses of the tuft; they branch freely and often have a characteristic appearance on account of the lateral shoots often arising almost at right angles. The internodes are usually short, and KJELLMAN refers *Sibbaldia procumbens* to one of the characteristic types of rosette-plants; in vigorous specimens from the Botanic Garden in Copenhagen the internodes are, however, as much as about one cm. long. The leaf-arrangement is two-rowed. The dead parts of the leaves persist for a long time on the shoot and may impart to the latter a peculiarly scaly appearance especially in its older parts; or the shoot becomes quite smooth owing to formation of periderm.

The floral shoots with the compact inflorescence are found during summer subtended by dead leaves which are seated below the living terminal rosette. Often 2—3 floral shoots are developed on the same branch. As is the case with the vegetative shoots, they vary greatly in size according to the nature of the habitat; in much exposed places they attain a length of 1—2 cm. only. — Plants which HARTZ collected at Scoresby Sound in the autumn had vegetative lateral shoots of the same year in which a small foliage-leaf had unfolded; in the Botanic Garden in Copenhagen this proleptic development is more pronounced. The new shoots begin either with a scale-leaf or with a weak foliage-leaf. Afterwards no scale-leaves are developed, and the shoot-apices are protected by the older, closely folding leaf-sheaths. The leaves wither in the autumn — at least in the Botanic Garden in Copenhagen.

Anatomy. The primary structure of the adventitious roots of the first and second order is practically the same, with the exception of the central cylinder which in the former is triarch-tetrarch and in the latter diarch. But the outer walls of the epidermis of the lateral roots are somewhat

stronger than those in the roots of the first order. The lateral roots have endotrophic mychorrhiza. The older roots are surrounded by a periderm which is formed in the outermost layer of the pericycle. The phelloid-cells occur in a few layers, and each series is separated by a layer of cork. Large intercellular spaces occur between the phelloid-cells themselves and between the latter and the next inner layer of cork.

In the rhizome there is formed during the first period of vegetation a complete ring of cambium which, however, does not produce a particularly large amount of secondary wood during the first year. With increasing age the latter reaches a considerable thickness and the continuous woody portion is very large; the annual rings in older rhizomes are not distinct. When older the rhizome becomes highly hyponastic. An endodermis is present. Periderm is formed during the first or second period of vegetation, after which the primary bark with epidermis dies and falls off. In the periderm one layer of cork alternates with about three layers of phelloid-cells. Specimens investigated from the Botanic Garden in Copenhagen had a smaller amount of cork in the periderm than the specimens from the other localities. Large intercellular spaces occur which are distributed as in the root. The outer, dead portion of the periderm persists as a very thick protective layer. Normally, no bast is produced in the rhizome, only in very vigorous specimens from the Botanic Garden in Copenhagen did I observe scattered groups of bast-cells. The pith is large and lives for a long time; it is, together with the periderm and the medullary rays, the chief depository of food-material. The starch collected during summer disappears, at any rate partially, during winter and is replaced by fat (Bot. Gard. in Copenhagen, January).

HOLLSTEIN has described the floral stem from material from the Dauphiné Alps. There occurred in the stems from these regions considerably more stereom than

in the stems from Spitzbergen and Greenland investigated by me. Within the epidermis, which had fairly strong outer walls, I found 1—2 layers of weak collenchyma; this was practically similar in the floral region and the rest of the stem, but the degree of development reached by the stereom in these two parts was different. In the floral region there were a great number of primary bundles within a common endodermis; secondary formations were of slight thickness only, as no interfasicular cambium occurred. The whole of the pericycle was transformed into bast of medium strength or weaker. In the rest of the stem a complete cambium had formed a considerable amount of secondary wood consisting chiefly of stereom, and in the pericycle isolated bundles of bast occurred. Here, also, there was a common endodermis.

Both leaf-surfaces are slightly hairy with compressed, unicellular, thick-walled hairs. Moreover, there occurred on both sides, but in greater abundance on the under side, small stalked glandular hairs of the form shown in figure 22, *B*. Stomata occur on both surfaces of the leaf in almost equal number; they are sunk below the level of the surface (Fig. 22, *A*). The outer wall of the upper epidermis is 3.3 to about 4 μ thick and that of the lower about 3 μ. The cuticle is uneven. The surface views of both the upper and lower epidermis have almost the same appearance, the radial walls are slightly undulating (Fig. 22, *E*, *F*). The inner wall of the epidermis of the upper surface is sometimes mucilaginous (Fig. 22, *C*). Cells with such mucilaginous walls are often larger than the surrounding cells (this fact is also mentioned by Warming in his "Halofyt Studier")[1] and they appear to occur in varying quantities in the different localities; in the leaves from the Botanic Garden in Copenhagen more epidermal cells were found with than without mucilaginous walls.

The thickness of the leaves showed some variation:

[1] See p. 59.

123 μ (Nunatsuk in Greenland), 154 μ (Gaaseland in Spitzbergen) and 174 μ (Botanic Garden in Copenhagen), and the proportion between the thickness of the leaf and the thickness of the palisade tissue was $\frac{2.2}{1}$, $\frac{2}{1}$ and $\frac{2.6}{1}$ respectively. The palisade parenchyma consists of 2—3 layers of cells.

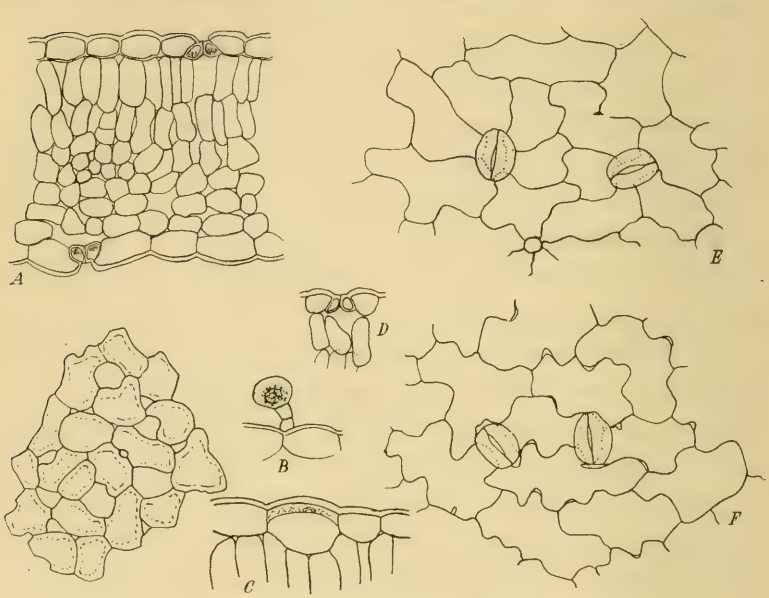

Fig. 22. *Sibbaldia procumbens.*

A, Transverse section of leaf; *B*, glandular hair from the upper surface of a leaf; *C*, epidermal cell from the upper surface of the leaf with mucilaginous inner wall; *D*, air-cavity below a stoma upon the upper surface of the leaf produced in part by the formation of a "Trichtercelle" (cf. text). *E*, Epidermis of the upper surface of the leaf; *F*, epidermis of the lower surface of the leaf, and *G*, section of spongy parenchyma. *A*, *B*, *C*, *D*, *E*, *F* and *G* $^{275}/_{1}$. *A*, *D* from Nunatsuk in Greenland, *C* from Godhavn in Greenland, *D*, *E*, *F*, *G* Gaaseland in Spitzbergen.

Below the stomata there is a large air-cavity which is formed either by the surrounding palisade-cells separating from each other at their upper ends, or by the adjacent cells tapering in the form of a funnel to the outside (Fig. 22, *D*). *Sibbaldia procumbens* may consequently be placed side by side with those specimens which RYWOSCH[1] mentions in support of his

[1] Beitr. zur Anat. d. Chlorophyllgewebes, Zeitschr. f. Bot., 1912.

theory as against HABERLANDT's, as regards the signification of the so-called "Trichtercellen" in the foliage-leaves; a theory which should more properly be called the WARMING-RYWOSCH's theory, as it corresponds with the views of the former investigator[1]) (see also *Alchimilla vulgaris* p. 108).

The polygonal or slightly branching cells of the spongy parenchyma are arranged in about four layers and include intercellular spaces which are usually smaller than the adjacent cells (Fig. 22, *A*, *G*). The bundles are not accompanied by stereom; the smaller branches are surrounded with a sheath while the larger ones are in addition accompanied by the usual vein-parenchyma, which compensates for the assimilatory tissue, up to both the upper and lower epidermis. In fresh leaves from the Botanic Garden in Copenhagen tannic acid occurred especially in the tissue of the veins and in both the upper and lower epidermis.

The insignificant flowers are collected in 6—12—flowered heads which consist of several small cymes. The petals are pale yellow and smaller than the inner sepals. The flowers are 7—8 mm. in diameter (WARMING's notes). The flowering period begins in July; NORMAN records July 9 for Arctic Norway, and at Scoresby Sound HARTZ observed the first flower on July 7. It no doubt usually sets ripe fruit. MÜLLER is of opinion that it has lost the power of spontaneous self-fertilization (Alpenbl., p. 222); WARMING, on the other hand, writes in 1886, that this cannot apply to the Greenland specimens because he found the anthers placed so close to the stigmas that self-pollination must no doubt easily take place (Fig. 23, *B*), and in his notes he remarks that the species is homogamous and that he has seen the anthers in contact with the stigmas. Similar observations are recorded by LINDMAN (1887) who investigated the species on Dovre

[1] Halofyt-Studier. Kgl. Danske Vidensk. Selsk. Skr., 6. Række, naturvidensk. og math. Afd. VIII, 4, p. 245. 1897.

(Scandinavia). He writes that the anthers are introrse and the filaments are bent inwards so that the anthers are separated by only ½ mm. or even less from the stigmas, and stand at a somewhat higher level than the latter; therefore

Fig. 23. *Sibbaldia procumbens.*

A, Flower seen from above. The disk (*d*) curves outwards between the stamens towards the petals (about $^{5}/_{1}$). *B*, Longitudinal section of a flower; the anthers are almost in contact with the stigmas ($^{6}/_{1}$). *C*, Carpel with germinating pollen and an anther with open pollen-sacs from flower from Kongsvold in Norway (about $^{20}/_{1}$). Drawn by Eug. Warming.

he thinks it is probable that self-pollination takes place. LINDMAN says that the flower agrees with MÜLLER's Fig. 87. As Fig. 23, *A* shows, there is a disk that curves towards the petals.

Dryas octopetala L. and **D. integrifolia** Vahl.

Lit. BUCHENAU and FOCKE, 1872. HOLM, 1885. WARMING, 1886, a; 1887. LINDMAN, 1887. KIHLMAN, 1890, p. 229. WAGNER, 1892. HARTZ, 1894, p. 48; 1895, a, pp. 288, 300 and 311; 1895, b. JÓNSSON, 1895. NORMAN, 1895. EKSTAM, 1897 and 1898. KRUCH, 1897. ABROMEIT, 1899. ANDERSSON and HESSELMAN, 1900. HESSELMAN, 1900. A. CLEVE, 1901, p. 45. DUSÉN, 1901. KNOTHE, 1902. SCHRØTER, 1904. HAGLUND, 1905. SIMMONS, 1906. SYLVÉN, 1906. HOLLSTEIN, 1907.

These two species are treated here jointly for brevity's sake, as they only differ in a few morphological and anatomical points. As regards their mutual systematic relation

the reader is referred to DRUDE[1], ABROMEIT (l. c.) and SIMMONS (l. c.)[2].

Dryas octopetala is circumpolar and is moreover found on the mountains of the temperate regions of Europe, in Asia and North America, in Iceland and the Færöes. *D. integrifolia* is found in Greenland, in Arctic America, where it has extended somewhat southwards, and in N. E. Siberia (cf. SIMMONS, where the distribution of both the forms is exhaustively discussed).

D. octopetala and *D. integrifolia* occur chiefly in dry localities, and NORMAN and A. CLEVE emphasize the fact that *D. octopetala* avoids damp localities in northern Scandinavia, and according to SIMMONS *D. integrifolia* does not thrive in damp soil in Ellesmereland. HOLM, however, observed *D. octopetala* growing in the Tundras of Nova Zembla. Heaths and rocky flats are their home proper.

The alcohol material was collected in Greenland, Iceland, the Færöes, northern Scandinavia, Spitzbergen and Nova Zembla.

DRUDE has included *D. octopetala* among his "Holzstauden" (Halbsträucher),[3] but both HAGLUND and SCHRØTER (l. c.) refer it to the dwarf shrubs proper, and their reason for doing so is that the destruction by frost during winter is not great and that the plant is woody and attains a very considerable age. Thus KIHLMAN (loc. cit. p .229) records that he has found a plant which was upwards of 108 years old. And SCHRØTER figures (Fig. 65) a shrub about 50-years-old which attained a length of about 1.60 metres. The growth is espalier-like[4] and the branches may be fixed to the soil by adventitious roots. WARMING remarks in his

[1] Die system. und geograph. Anordnung der Phanerog. in SCHENK: Handbuch der Botanik, III, 2, pp. 212 and 256, fig. 1.
[2] Fig. 24 represents different leaves of an intermediate form.
[3] Handb. d. Pflanzengeographie, 1890.
[4] WARMING's term for prostrate, outspread growth.

notes as regards D. *integrifolia* in Greenland, that it grows in flat, low tufts, usually almost circular in form and about a foot or so in diameter. Each tuft has a strong main root, and a few slender, weak adventitious roots arise from the branches. From the upper end of the main root the branches proceed laterally in a horizontal direction, and they may become fairly long. It hardly propagates vegetatively. — In *D. octopetala* from Russian Lappmark KIHLMAN (l. c.) measured branches which were about two metres in length. HAGLUND ascribes to *D. octopitala* a rich formation of adventitious roots from the prostrate parts of the shoots, according to him it is almost exclusively the adventitious roots, which provide the older individuals with nourishment; he has not been able to find a persistent main root. SCHRØTER records a rich supply of adventitious roots from the under side of the branches of *D. octopetala* in the Alps. In WARMING'S notes we read further as regards *D. integrifolia*: "The shoots are close-set and among them masses of dead leaves are found which persist several years; it grows in its own remains; the fresh shoots are seen in the midst of the blackish brown remains of old leaves. Large patches may be found dead in a tuft, but the leaves are still densely crowded."

Fig. 24.

Leaves of a form intermediate between *Dryas octopetala* and *D. integrifolia* collected at Kingigtok in Vaigat by Hartz. All the six leaves were found on the same plant, and the different forms were represented almost to an equal degree (about natural size).

The young seedling of *D. octopetala* has been described by HAGLUND and SYLVÉN; it forms a rosette which is provided with a main root and which sooner or later develops lateral shoots. The structure of the shoot of the full-grown plant has been treated by HAGLUND (loc. cit. p. 7) who, however, doubtfully refers *Dryas octopetala* to dwarf shrubs

with racemose shoot- structure, citing as additional examples *Cassiope tetragona* and *Empetrum;* and on p. 33 he says that there is a clear distinction between vegetative or vegetative-floral short shoots and vegetative long shoots. In Lappmark where he was staying the long shoots measured 2—4 cm., and had spirally arranged leaves in the axils of which short shoots developed even during the same year. Ascherson and Graebner[1] ascribe to *D. octopetala* a long and much branching stem with prostrate long shoots and numerous erect short shoots. — The results of my investigations of *Dryas octopetala* and *D. integrifolia* are in several respects different from those arrived at by Haglund.

The same year in which a shoot flowers it produces a small number of usually close-set lateral shoots, as generally only the upper leaves subtend shoots. At first the shoots have a scale-leaf, afterwards foliage-leaves follow. In vigorous and luxuriant plants the shoots are usually distinguished into short shoots and long shoots, which otherwise behave as described by Ascherson and Graebner. In investigating shoot-apices in plants both in the Botanic Garden in Copenhagen and in the alcohol material, small flower-buds were as a rule found on all shoots gathered in the autumn: when such were absent the shoots were frequently weak short shoots. Fig. 25 shows a longitudinal section through a flower-bud gathered in August in Greenland; the stamens have just been developed and there are indications of the outermost carpels. The young flowers in the Botanic Garden in Copenhagen had in January developed so far that the stamens were externally fully developed, but in the carpels no ovules were formed. Probably the development is not so advanced at the same time in colder regions where the flowering period also occurs later than in Copenhagen (see

[1] Synopsis d. mitteleurop. Flora. VI, 1, pp. 889—90.

p. 73). It is not, however, by any means all the flower-buds that are formed which reach maturity. In Copenhagen numerous dead buds were found during autumn and winter. Otherwise such shoots with a dead apical flower-bud behave as do those that flower. The above-mentioned weak shoots which do not at once produce buds, may do so after having lived through one or perhaps several years of growth in vigour, but I also find that such shoots may after the lapse of a few years die in a purely vegetative stage, probably suffocated by the more vigorous shoots overshadowing them. HAGLUND writes that the short shoots immediately put forth new short shoots, and this is undoubtedly often true. I must regard the short shoots in *Dryas octopetala* and *D. integrifolia* simply as shoots which have become weakened by competition among themselves, and it is undoubtedly normal for the shoot-development to end with flower-formation. According to the above the branch-system in *Dryas*[1] is sympodial, a few new shoots being produced every year; of these usually one or two are more vigorous than the others.

Fig. 25. *Dryas octopetala.*

Median section through a young flower-bud which would not have attained the flowering stage until the following summer (Kingigtok in Vaigat; Aug. 2; $^{25}/_{1}$); *c*, indication of carpels; *st.*, young stamens; *p*, petal; *sp*, sepal.

The length of the long shoots naturally

Fig. 26. *Dryas octopetala* (Iceland). 16. 1. 1894.

a. A shoot-apex which shows how the rolling back of the leaves increases towards the apex of the shoot; the uppermost leaves are living the older are dead; *b*, a leaf seen from the lower surface; *c*, a highly revolute leaf seen from the lower surface (Helgi Jónsson's figures l. c.).

[1] The North American and the North-east Asiatic *Dryas Drumondii* Richards. behaves in a similar manner.

varies greatly; I have found them to be from one to about 10 cm. long; the longest are often found at the periphery of the tufts.

Haglund (l. c.) records that the leaves of *D. octopetala* die away during winter; others find that the leaves remain green during winter, viz. Schroter, Hartz (1895*a*, p. 182) and Jónsson (cf. Fig. 26); in my material there were specimens collected by Jónsson in January, and they agreed exactly with his figure and in this manner *D. octopetala* also behaves in the Botanic Garden in Copenhagen. Finally, Warming remarks in his notes that *D. integrifolia* has leaves which live through the winter. The oldest leaves on the shoot wither in the autumn but as figure 26 shows there are a few half expanded young leaves at the apex of the shoot and these live through the winter. Scale-leaves are not developed (cf. Haglund); the shoot-apices are protected by the leaf-sheaths.

Anatomy. The root-system as mentioned above is characterized by a vigorous main root which bears vigorous branches. The absorbent roots are richly branched and their apices are encompassed with a thick mantle of fungal hyphæ. Hesselman figures mycorrhiza of *D. octopetala* which resemble those of the *Cupuliferae: D. integrifolia* also has mycorrhiza. Hesselman also illustrates the structure of the root by several figures.

The central cylinder in the primary root is surrounded by a vigorous endodermis and in the innermost layer of the cortex the radial walls are highly thickened in the middle, so that the transverse section of the wall shows an almost circular figure. Periderm is developed in the outermost layer of the pericycle, and gradually as the periderm and the secondary wood grow the cortex dies and is thrown off together with the hyphæ. In older roots it attains a considerable thickness; it consists exclusively of cork-cells which

often have somewhat curving tangential walls. There are no intercellular spaces in the periderm. The older roots consist mainly of secondary wood with medullary rays of one layer and several cells high which are united with one another by tangential bands of wood-parenchyma containing starch.

In the young shoot there are 3—5 primary vascular bundles. The cambium begins its activity quickly and in the first period of vegetation it forms a considerable quantity of wood. There is no endodermis, as HOLLSTEIN also has noticed. Outside the primary sieve-tissue, and afterwards also outside the secondary, bast is developed, usually in isolated groups, rarely as a continuous ring. The secondary bast is often present in less quantity than the primary, naturally enough, as the woody part affords sufficient support. In the Botanic Garden in Copenhagen there always occurred a more strongly developed bast than in plants from more northern regions. The cortex is of simple parenchyma and the epidermis is small-celled and has strong outer walls, about 3 μ thick, with a well-developed smooth cuticle. The pith is heterogenous. There is a peripheral part of active, starch-containing cells and in the central part similar cells form a network between larger and dead cells. The active tannin-containing pith-cells have strong walls.

Shortly after the cambium has begun to develop wood a phellogen arises in the cortex outside the bast. The first phellogen forms a cylinder which may be closed, but afterwards a typical crust-bark, "Schuppenborke" (cf. HOLLSTEIN) is formed. Each phellogen produces 3—4 layers of cork, and each new phellogen-layer cuts off a portion of the secondary cortex with the bast-groups or bast-cells enclosed in it. The primary, but dead cortex may be found on the branches even during the third year, and 5—6 cork-plates may be counted, separated by dead cortical tissue.

The secondary wood often, but by no means always, shows distinct annual rings. The growth-increment of the first year is equally vigorous on all sides, but afterwards the branch becomes highly hyponastic. The yearly growth on the hyponastic side is naturally very different in different localities; but it was always found to be less in the Arctic and Subarctic material of *D. octopetala*, on an average 0.2 mm. in younger branches, than in plants from the Botanic Garden in Copenhagen where the average growth, likewise for younger branches, was found to be 0.9 mm. Kihlman found an average yearly growth of 0.07 mm. in the 108-years-old branch mentioned above, and Schroter measured a yearly mean growth of 0.22 mm. in a 50-years-old stem from the Alps. The maximum of the radial vessel-diameter was also greatest in specimens from Copenhagen. — The chief depository for reserve food-material in the two *Dryas* forms is naturally the branches, and the tissues containing starch are, in addition to the active part of the pith, the medullary rays, which may be as much as 3 cell-layers thick, and several cells in height, and here as in the root are connected by tangential bands of wood-parenchyma. During winter the starch disappears from the branches almost entirely and is replaced by fat. In Copenhagen this change took place in November.

In the peduncle there are no secondary formations. Outside the numerous (about 20) primary vascular bundles there is gradually formed a strong bast-cylinder which is correlated with the fruit-bearing function of the peduncle; there is no endodermis. The active cells in the pith have weaker walls than have those in the stem.

The leaf in *D. octopetala* and *D. integrifolia* is leathery and especially in the former is highly reticulated upon the upper surface. The lower surface is silver-white with a dense felt of hairs; the upper surface is usually glabrous, but in several forms it may be more or less hairy; for instance in *Dryas*

octopetala γ, *hirsuta* Hartz and δ, *argentea A* Blytt, in the latter the upper surface is densely woolly, and *Dryas integrifolia* var. *canescens* Simm., in which the upper surface is densely tomentose. The leaves are revolute in the bud-condition and also as a rule, to a greater or less degree, when full-grown, especially in *D. integrifolia* (Fig. 27, *A*). In this respect it is of importance whether the plant grows in favour-

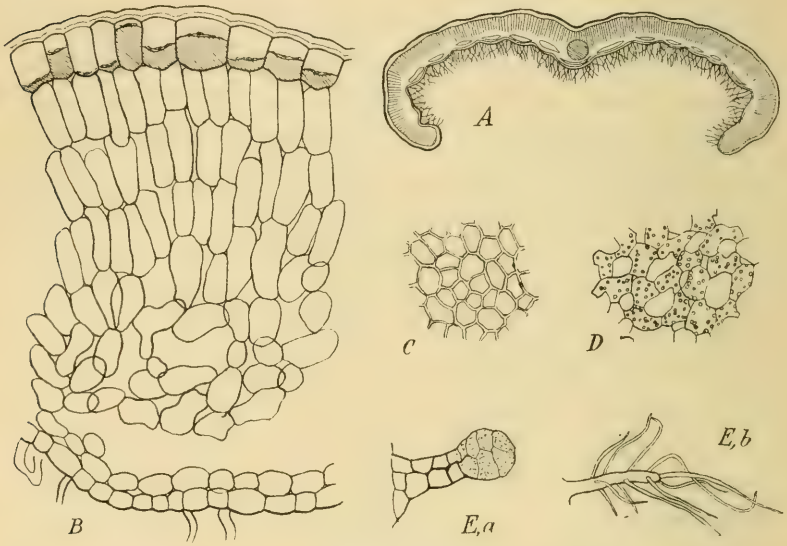

Fig. 27.

Dryas integrifolia. *A*, Transverse section of leaf; $^{20}/_{1}$ (Eug. Warming, 1887). *B*, Fragment of transverse section of leaf $^{220}/_{1}$). *C*, Surface view of epidermis of the upper surface ($^{140}/_{1}$). *D*, Section of the spongy parenchyma of the leaf ($^{190}/_{1}$). — *Dryas octopetala.* *E*. Hairs from the bundles on the upper surface of the leaf; *a*, glandular hair ($^{200}/_{1}$); *b*, branched hair ($^{50}/_{1}$).

able or unfavourable localities. Thus the most revolute leaves are met with in dry rocky flats or on downs (Dove Bay in N. E. Greenland). Even in one and the same tuft there may be differences as regards the degree to which the leaf is revolute. HARTZ (l. c. 1895 *a*, p. 311) figures a tuft of *D. octopetala* β *minor* from East Greenland, and writes regarding it that "to windward the branches are stunted and decorticated,

the leaves are torn off or extremely small, and linear with involute leaf-edges; the leaves to the leeward of the shrub are larger and their leaf-edges are involute in a less degree or not at all." Hartz gives in the same place some information regarding the habitats of the different forms in East Greenland. Thus he found *D. octopetala α genuina*, which has large broad leaves, in damper localities in sheltered spots, and it was covered with snow during winter, while *β minor*, which had small narrow leaves, *γ hirsuta*, *δ argentea* and *D. integrifolia* were found in dry localities, and were usually not snow-covered during winter. The young leaves which live through the winter are so highly revolute that the lower surface is almost entirely covered. Warming remarks in his notes that the leaves when dry roll back towards the condition of the bud-stage, but on getting wetted they spread out again. As the stomata only occur on the lower surface the importance of the revolute condition is easily understood.

The epidermis of the upper surface has a very strong outer wall which is somewhat thicker in the winter leaves than in those of the summer. Thus in the latter it was found to be 2.5 μ (Iceland and Copenhagen), 4.4 μ (the most common) and 6 μ (*D. octopetala* from downs at Dove Bay in N. E. Greenland) and in the winter leaves 6—7 μ (*D. octopetala* from Danmarks Ø off East Greenland) and 8 μ (Iceland). The cuticle is considerable; it is smooth and the cutinized portion constitutes above one-half of the wall; its inner limit is distinctly toothed (Fig. 27, *B*). Kruch (l. c.) records that in *D. octopetala* the walls of the upper epidermis are mucilaginous; this I also have found to be the case, though not in all the cells; on the other hand, he denies the presence of mucilage in *D. integrifolia*, but this difference I have not been able to verify (cf. Fig. 27, *B*). The palisade parenchyma is very thick and is composed of about three layers of cells. The spongy parenchyma is rather loose and consists of slightly branching cells (Fig. 27, *D*).

The epidermis of the lower surface together with the subepidermal layer is as a rule separated from the rest of the leaf-tissue by large slit-like lacunæ occurring between the larger bundles (see Fig. 27, *A*, *B*). HOLM (l. c.), who has described and figured the anatomy of leaves from Nova Zembla, mentions similar lacunæ.

According to HOOKER (Fl. Bor. Amer.) the veins in the leaves of *D. octopetala* are distinctly visible on both sides of the leaf, and the upper surface acquires thereby a somewhat wrinkled appearance, while in the leaves of *D. integrifolia* they are only slightly or not at all visible, and therefore the upper surface is smooth. Also as regards the anatomy there is a difference in the leaves of the two forms in connection with the bundles, there being in the leaf of *D. integrifolia* less chlorophyll above and below the bundles than in the leaf of *D. octopetala*, so that the transverse section of the former shows as many bright transverse bands as there are larger bundles, while this appearance is far less distinct in *D. octopetala*. In other words, the vein-parenchyma is more strongly developed in *D. integrifolia* than in *D. octopetala*.

The stomata are situated on a level with the surface and occur especially in the spaces between the bundles. — The majority of the hairs are unicellular, they are erect and intertwining and form thereby the dense, thick layer of felt (Fig. 27, *A*). Upon the larger bundles which project as ribs the felt-hairs are partially wanting, but here large, several-celled, branched hairs and several-celled glandular hairs occur (Fig. 27, *E*).

During winter the chlorophyll takes up in a marked degree the winter-position described by KRAUSE. In the palisade-cells it gathers in the inner part, and in the cells of the spongy parenchyma it retires from the parts of the walls which border on the intercellular spaces.

The two species of *Dryas* flower generally very abundantly;

they appear to agree as regards the structure and the biology of the flower. Warming (l. c. 1886 *a*, pp. 127—28) has described and figured the flower of *D. integrifolia*. He writes: "that as *D. octopetala* (in Norway, Spitzbergen and the Alps) this also has hermaphrodite and male flowers and from a biological point of view they appear on the whole to resemble each other exactly." — Fig. 28 is a reproduction of his figure: *A* shows a branch with the terminal flower; *B*, a hermaphrodite flower; *C*, a male flower, at the base of the hypanthium of the latter are seen some pistil-rudiments. — "As in *D. octopetala* the hermaphrodite flowers are larger than the male flowers, but the smallest forms of the former are somewhat smaller than the largest of the latter"[1]. — According to Simmons (l. c.) the flower of *D. integrifolia* is on an average somewhat smaller than the average size of the flower of *D. octopetala*. — "The petals (8—11) are white or yellowish-white while young, but with increasing age become darker yellow or brownish yellow." — In *D. octopetala* they are almost pure white (Simmons). — "It appears that the hermaphrodite flowers may be both homogamous and slightly proterogynous or slightly proterandrous; on July 15, 1884, I gathered near Amerdlokfjord (W. Greenland) flowers, the anthers of which were open while the styles were still short, and the stigmas appeared to be quite immature; in other cases the pistils are very long and have ripe stigmas while the stamens are still lying bent inwards with closed anthers (Fig. 28, *D*); lastly there are cases where the anthers and stigmas begin to function simultaneously and as they are at the same level or the anthers are slightly higher than the stigmas and very close to the latter or rise above them, self-pollination will easily be able to take place; I have even repeatedly observed the anthers to be carried in between the stigmas." "Honey is secreted by the inner side of the hypanthium (the shaded part of the

[1] A similar case is described by Müller in Alpenbl., p. 227.

figures). The stigmas are not very conspicuous or delimited from the rest of the smooth upper part of the style (Fig. 28, *F*)." LINDMAN has investigated *D. octopetala* on the Dovre (Scandinavia) (l. c. Tab. III, Fig. 30). AXELL[1] mentions polygamy, writes LINDMAN, but he himself found hermaphro-

Fig. 28.

Dryas integrifolia. *A*, *B*, *C*, *D*, See text. *E*, Pistil. *F*, Apex of style with germinating pollen. *G*, Anther (Warming, 1886 a). — *Dryas octopetala*. H, Rudimentary carpel of a male flower from Bosekop (Arctic Norway; $^{13}/_{1}$).

dite flowers only. In the flowers he investigated he found proterogyny to be more decidedly pronounced than is the case in Central Europe according to RICCA (Att., XIV, p. 253) and MÜLLER (Alpenbl., p. 227). LINDMAN does not mention proterandry. EKSTAM (1897) records *D. octopetala* from Nova Zembla; the diameter of the flower was 10—25 mm., the

[1] Om Anordningarna för de fanerog. växternas befrugtning, 1869.

flowers had no perfume, and he found homogamy only. Self-pollination is made possible by the fact that the anthers bend over the stigmas or towards them. In 1898 the same author writes regarding the flowers from Spitzbergen; here the diameter was found to be 20, 25, 27 mm., exceptionally 28, 32, and even 38 mm. (Müller records the diameter of the flower in the Alps to be 27—40 mm.; l. c.). Self-pollination may easily take place as the anthers shed the pollen immediately upon the stigmas. Honey is secreted between the androecium and the gynoecium. Lastly, Dusén describes the flower-biology in East Greenland between 70° and 75°. He found *D. octopetala* to be homogamous; regarding *D. integrifolia* he writes that it is "dioecious (♀)."

In my material were 18 flowers (preserved in spirit) from Bosekop in Arctic Norway (collected by Warming, 1885), of these four were male, the others hermaphrodite: one of the latter showed a distinctly proterandrous stage: almost all the stamens had raised themselves into the air and had opened their anthers, while the pistils were yet without papillæ. The others were in a homogamous stage. Fig. 28, *H* shows a rudimentary carpel from Bosekop; the ovule with the embryo-sac is formed. Moreover, the material contained four flowers gathered by Holm at Mejduscharskji(?) and probably from Nova Zembla; three of these were distinctly male, the rudimentary carpels did not rise above the hypanthium. In the material was also found a male flower from Lille Snenæs in East Greenland.

The insect-visitors in northern regions appear chiefly to be flies and similar diptera (Lindman, Hartz and Ekstam).

D. octopetala and *D. integrifolia* flower in early and middle summer (June and August; Lange, Norman, Ekstam, Andersson and Hesselman, and Simmons), and Ascherson and Graebner (l. c.) record, as regards Central Europe, (May) June and August. In Ellesmereland *D. integrifolia* is one of

the earliest flowering species (SIMMONS). The Scandinavian Floras, on the other hand, record July, August.

Usually fruit is set abundantly and regularly; as regards Spitzbergen ANDERSSON and HESSELMAN write, however, that fruitsetting is sometimes irregular, and in northern Sweden the fruit does not ripen at a height of 1000 metres above sea-level (A. CLEVE). NORMAN (l. c.) often finds empty fruit without kernel.

The fruit dispersal is decidedly anemophilous. The highly elongated and densely hairy styles in the ripe fruit spread themselves out in dry weather, but in damp weather they again unite into a single cone usually twisted to the right. The peduncle elongates considerably during fruit-setting and attains double its usual height (EKSTAM, 1898).

Rubus saxatilis L.

Lit. WARMING, 1884 and 1886, b. NORMAN, 1895. POPPIUS, 1903.

This species is not really Arctic; it is found in Greenland, but south of the Polar Circle, in Iceland, the Færöes, in Central and North Europe (also north of the Polar Circle), Siberia and in Caucasia (LANGE).

The alcohol material was collected in Greenland, Iceland and in several places in Denmark.

The shoots have a two-years period of development. In the first year a shorter or longer scale-leaf-bearing shoot is formed, which is erectly ascending or has an oblique lateral growth; it lives through the winter with its apex at the surface of the ground; next year the aerial shoot is formed. The length of the shoot of the first year is dependent on the distance of the subtending leaf from the surface of the ground, and also on the nature of the soil; as may be expected, in the loose leaf-mould of woods longer shoots are developed (Fig. 29, *A*), while in harder soil the shoots are often quite

short. In conformity to this the rhizomes which persist for several years are shaped very differently. The scale-leaves are two-rowed as are the leaves of this species generally. There appears to be a difference between the upper and lower rejuvenating shoots, only the upper having been found to be floral, and those of them, which had not been proleptically developed in the same year as the parent-shoot, develop at the end of summer flower-buds for the next year (Fig. 29, *A*, *C*). I have not found flower-buds on the lower and longer shoots. Next year the flower-buds produce first 2—6 foliage-leaves and then the flowers expand, but the vegetative propagating shoots produce first an

Fig. 29. *Rubus saxatilis.*

A, Shoot-base from Denmark (Oct. 22, 1912). The plant has been growing in loose leaf-mould and has therefore especially elongated internodes. The lateral shoot *a* was floral and would have flowered in the summer of 1913, while the two other shoots, at any rate the strongest, *b*, would have produced assimilatory and wandering shoots. The buds *a* and *b* reached the surface of the ground. Lowermost in the figure is seen the upper part of the shoot from 1911; there are dormant buds in the axils of the scale-leaves (slightly above natural size). *B*, Stolon-apex from Denmark (Oct. 1912). Just at the point where the stolon bends the axis is somewhat thickened, and from here numerous vigorous adventitious roots arise (slightly above natural size). C, Longitudinal section through the bud *a* in Fig. A; the exterior of the stamens well-developed, but the pollen was found not to have developed yet; nor had the ovules begun to develop in the carpels ($^{50}/_{1}$).

erect lower portion like the floral shoot and then creeping runners. The runners have elongated internodes, small leaves, and develop no roots; from the leaf-axils other runners arise. Towards the end of summer the apex of the stolon slightly penetrates the ground; it then becomes negatively geotropic, the internodes shorten and scale-leaves are developed. The stolon is somewhat thickened at the point where it bends and thence long, vigorous and richly branching roots arise (Fig. 29, *B*). These shoots also pass the winter at the surface of the ground. According to WARMING (1884) the stolons may attain a length of 1½—2 metres. In Arctic Norway they are, according to NORMAN, often above 2 metres, and he places the maximum at about 4 metres. During autumn the aerial shoots die away, at any rate partially, and the terminal buds of the stolons are set free and become independent individuals.

The structure of the shoot in *Rub. saxatilis* may be produced through a slight modification of the type common among the *Eubatus*. As the stolons live through one summer only, the flower-buds are placed near the surface of the ground, and new shoots arise from the base of the floral shoots as well as from the wandering shoots. Moreover, e. g. in Denmark, specimens are met with which form a transition between the two types, as they enter the winter with living shoot-bases, a few cm. long, which protrude above the ground and bear flower-buds.

Anatomy. Of roots only those adventitious roots have been investigated which arise from the apex of the stolons. The epidermis in the roots of the first order is thin-walled, while the subepidermal layer has stronger, brown walls. In the roots of the second order the epidermis has thicker outer walls, and the exodermis is not so well-marked. The central cylinder is in the former tetrarch and in the latter diarch. The roots of the second order are particularly characteristic owing to the structure of the cortical layer

which is situated just outside the endodermis, the radial walls appearing as thick, refractive, non-stratified cushions (Fig. 30, *E*). Also in roots of the first order a similar structure has been found, but it is less common there. The periderm is formed during the first period of growth in the outermost layer of the pericycle at the same time as the primary cortex dies.

The stem is covered with a fairly dense layer of unicellular, thick-walled hairs; sometimes a few weak spines occur. The axis-system in this species illustrates fairly well how highly the development of the different tissues is dependent on the length of life and the function of the different parts of the stem. In the erect part of the stem no periderm occurs, with the exception, however, of the lower scale-leaf-bearing part which as already mentioned becomes at any rate partially perennial. In the first year it consists here of only about three layers, which develop immediately outside the bast in the cortex as is the case in the species of various other groups of *Rubi* investigated by Fritsch (l. c.). In the stolon the same features occur as in the stem of *Rub. arcticus;* a phellogen is developed which probably does not become functional. On the other hand, in the somewhat thickened apex of the stolon a fairly well-developed periderm is found towards the end of summer, in correlation with the altered conditions. In Denmark it consists chiefly of phelloid cells which at that time when the bud begins to become independent, contain a large quantity of starch. Also in the perennial subterranean axis the periderm, which is 10—15 layers thick, consists chiefly of phelloid, at any rate in Denmark in humus soil, while the periderm in the Iceland specimens was richer in cork. The periderm rich in phelloid makes a spacious reservoir of food-material. It contains small intercellular spaces. I have seen no endodermis either in the rhizome or in the aerial stem.

Bast-tissue is absent from the rhizome; it is most vigorously developed in the stem where it forms a continuous cylinder outside the sieve-tissue; the bast is connected with the secondarily formed portions of stereom in the outer part of the groups of wood by the lignified medullary rays. The stolon also contains bast abundantly; it is more slightly developed in the thickened apex.

In the rhizome a continuous cambium forms a continuous woody portion which shows distinct annual rings. The numerous medullary rays are 1—3-layered and upwards of 20 cells in height. In the stem there is no continuous cambium except in its basal part; on the other hand a continuous cambium begins to function early in the thickened apex of the stolon.

While the cortex in the stem is distinguished into an outer small-celled part filled with chlorophyll and an inner larger-celled part poor in contents, the whole cortex in the apex of the stolon functions as food-storing tissue, and is crowded with starch in the autumn. The 1—3 outer cortical layers are collenchymatous especially in the erect stem.

The pith is heterogeneous as in all the *Rubus*-species hitherto investigated (cf. FRITSCH). The active cells, especially the starch-containing ones in the rhizome and the apex of the stolon, are found chiefly in the periphery of the pith, but also in addition dispersed longitudinal rows of living cells occur in the central part which for the rest consists of larger dead cells. Anastomoses are rare.

During autumn the quantity of starch diminishes in the different tissues of the rhizome and at the same time large quantities of fat may be demonstrated.

The leaves are slightly hairy on both sides and are somewhat folded. No glandular hairs were found. On the lower surface the bundles are very prominent. The structure is mesophilous in correlation with the fact that the leaf lives

one summer only, and is moreover strongly influenced by light The leaves from Greenland (Tasermiut-Fjord) had the following dimensions: Thickness of leaf 110 μ, thickness of the outer wall in the upper epidermis about 3 μ,

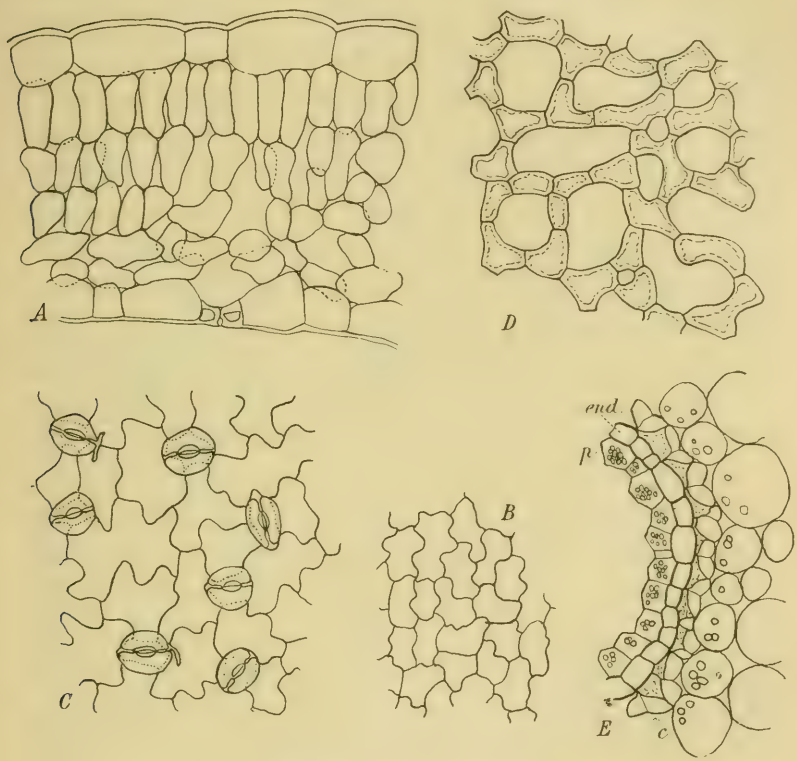

Fig. 30. *Rubus saxatilis.*

A, Transverse section of leaf. *B*, Epidermis of the upper surface of the leaf. *C*, Epidermis of the lower surface of of the leaf. *D*, Section of the spongy parenchyma of the leaf parallel to the surface. *E*, Fragment of an absorbent root of second order; *c*, the cortex, the radial and outer tangential walls of its innermost layer have highly thickened walls; *end*, endodermis; *p*, outermost layer of the pericycle. A, B, C, D from Greenland, E from Denmark (*A*, *C*, *D*, *E* $^{280}/_{1}$; *B* $^{130}/_{1}$).

in lower epidermis about 2 μ, the corresponding dimensions from leaves collected in Iceland (Aðalvik in N. W. Iceland) were : 130 μ, about 4 . 4 μ and about 3 . 3 μ. An explanation of these differences is suggested by the vague

records on the labels: The Greenland specimens are said to be collected "under and between birch copses," consequently, most likely on shady ground, while those from Iceland grew on "Lien" (grassy slopes), consequently, probably in more open ground. Leaves collected in very shady localities in Denmark were about 90 μ thick and had in a high degree the character of "shade leaves," with only one layer of palisade-cells, which were funnel-shaped, and a few layers of spongy parenchyma. The proportion between the leaf-thickness and the thickness of the palisade tissue was about $\frac{2}{1}$ in leaves both from Greenland and Iceland. The figures show the leaf-structure of the common type; a loose palisade parenchyma consisting of 2 layers of cells ,about twice as high as broad, and a likewise very loosely built spongy parenchyma. The stomata occur only on the lower surface of the leaf; they are situated on a level with the surface. (Fig. 30, *A*, *B*, *C*, *D*.) — Bast-tissue is absent from the leaf.

Three distinct bundles enter the leaf-stalk (see p. 87); shortly afterwards the two upper lateral ones divide each into two bundles of which the lower one on both sides gradually approaches the median lower bundle and ultimately fuses with the latter the transverse section of which then becomes crescent-shaped. The fusion takes place a short distance above the point where the sheath ends, and in the rest of the stalk there are 3 bundles. The two upper are round in transverse section and lie in the ribs which form the furrow on the upper surface of the stalk; the two latter especially are accompanied by a strong fibrous tissue.

The flower-biology has been investigated by WARMING (1886, *b*). He writes (loc. cit. p. 40) "The petals in the latter (*Rub. saxatilis*) stand erect, and the stamens bend somewhat toward the centre without however uniting so closely together above it as in *Rub. arcticus;* there is, at any rate in a somewhat older flower, an entrance between them

down to the pistils; they have similar finely warted filaments to those of *Rub. arcticus* (Fig. 37), which likewise terminate abruptly above in a smooth and much thinner portion, and in my opinion the pollen from them must certainly fall upon the stigmas." H. Müller (Alpenblumen, p. 216) arrives at the same conclusion. (Compare Fig. 31). Warming states in his notes that the stigmas become functional very early: even in the hardly expanded flowers from Talvik in northern Norway they are highly papillose; the outermost stamens are the next to become functional and afterwards the others. But

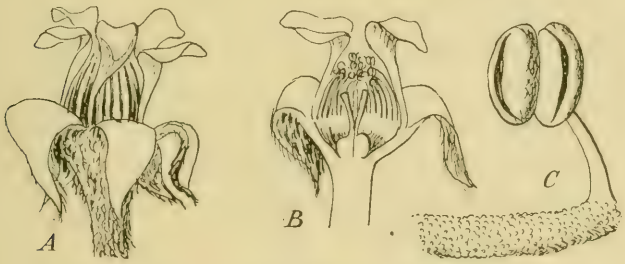

Fig. 31. *Rubus saxatilis* (Talvik in Arctic Norway).
A and *B*, Flowers (about $^3/_1$); *B*, in longitudinal section. *C*, A stamen (about $^{25}/_1$); cf. text. Drawn by Eug. Warming.

even if the flowers have perhaps at that time a short proterogynous stage, they become homogamous at any rate early. As regards the supposed importance of the warts on the filaments see *Rub. arcticus*, p. 97. Poppius (l. c.) records that in Finland *Rub. saxatilis* is eagerly visited by *Vespa vulgaris* L.

The flowering begins in Scandinavia in June; Norman records June 21. In some years it does not set fruit in the northern districts of Arctic Norway. The fruits may be ripe on July 28 (Norman). In Greenland it is usually found without fruit, and in the Færöes it sets fruit sparsely.[1]

[1] Ostenfeld, Planteväxten paa Færöerne, København, 1906.

Rubus chamæmorus L.

Lit. WARMING, 1886, a. LINDMAN, 1887. KIHLMAN, 1890, pp. 55, 113. HARTZ, 1894, p. 7. NORMAN, 1895. KOLDERUP ROSENVINGE, 1896, a. KRUCH, 1897. ANDERSSON and HESSELMAN, 1900. A. CLEVE, 1900, p. 47. POPPIUS, 1903. SYLVÉN, 1906.

Rubus chamæmorus is circumpolar, but thrives also in temperate regions in Asia, America and Europe, where in many places it must most properly be regarded as a relict. It occurs almost everywhere in damp localities, and grows by preference on the loose surface of bogs and marshes. A few exceptions from this rule are however known, the plant in Arctic Norway, according to NORDMAN, growing in dry localities furthest out towards the sea and especially at some height above it; an explanation of this phenomenon has been sought in the fact that the air from the sea is extremely damp. In Greenland also, where it only occurs in the coastal districts and on islands in the skerries, it grows on relatively dry and heath-like tracts.

The aerial shoots are vegetative or vegetative-floral. They usually bear 1—3 foliage-leaves and are terminated by a solitary flower or by a dead bud enclosed in the sheath of the uppermost foliage-leaf. The aerial shoot usually has at its base a few scale-leaves with intervening short internodes (Fig. 32, *C*). The uppermost of these scale-leaves are doubtless as a rule situated above the surface of the bog, and often from the axils of the lower arise during summer scale-leaf-bearing shoots which will next year produce aerial shoots. Consequently, the plant has a two-years development. During autumn the scale-leaf-bearing shoots form a distinct resting-bud which is situated at the surface of the bog. If the shoot arises from a point which is situated at some depth in the bog it assumes a more or less decided wandering stage before it enters into the assimilatory or ultimately floral stage; the shoot to the right in Fig. 32, *D*

exemplifies this; but the development is nevertheless of two years duration. The plant has, however, a much greater power of wandering, because it gives off horizontal runners which may attain a length of above 30 cm. Fig. 32, *A*, *B* are apices of the latter in the wandering and resting stages respectively. These well-marked wandering shoots arise from deeper-lying parts of the plants, and their two-rowed sheath-

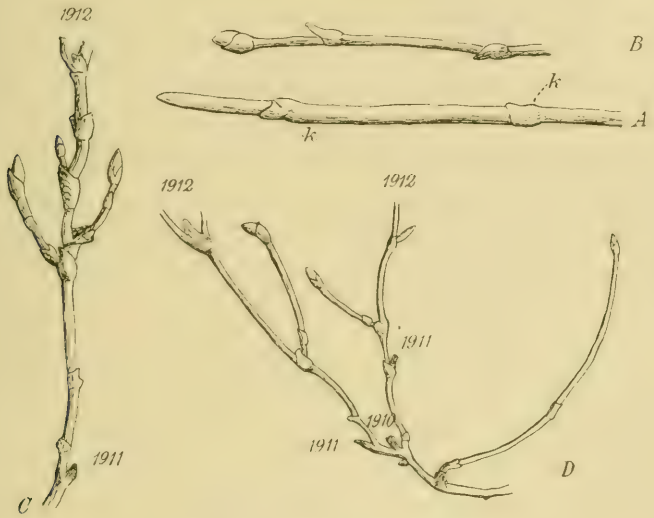

Fig. 32. *Rubus chamæmorus.*

A, Apex of a runner (Norway; July 22); *k*, bud. *B*, Runner with resting bud in which the first foliage-leaf is formed (Denmark; Oct. 6). *C* and *D* are branch-systems in the winter-stage (Denmark; Oct. 6). The shoots marked *1912* have that year been assimilatory shoots, from their base new shoots arise bearing winter-buds. Portions of axes marked *1911* and *1910* have been assimilatory during these years. All the figures are about natural size.

like scale-leaves may subtend new runners. In the beginning of autumn they may either develop a resting bud which is situated almost at the surface of the bog and which in Denmark in October contains the first foliage-leaf of the assimilatory shoot of the next year, or the runner may live through the winter deeper down in the bog without developing a resting bud proper and next summer resume its

wandering life. The shoot then takes more than two years to develop. When a runner is entering on its last stage it grows upwards toward the surface of the bog and at the point where it bends the internodes usually become somewhat shorter, but by no means always, as easy transitions from runners with 3—4 short internodes at the bending point to runners which form aerial shoots without any shortening of their internodes are met with. This difference expresses the state of dependence in which plants growing in a bog stand to the moss-vegetation of the latter. The shoots, without the shortening of the internodes, were probably in danger of being overgrown by the moss, consequently, no short internodes have been formed but only elongated ones to carry the terminal bud upwards to reach the light.

The older plant probably develops only adventitious roots; the latter arise from the nodes of the runners during the second period of growth.

Among related species this *Rubus* has no doubt an unique shoot-structure which appears to make it specially adapted for life in the habitats it has chosen for itself.

Anatomy. The adventitious roots are diarch—tetrarch. The endodermis has rather thick walls which have become corky. Even before the periderm, which is developed in the outermost layer of the pericycle, is formed, consequently, in the absorbent-root stage, the epidermis is destroyed and the two outer layers of the cortex assume the appearance shown in Fig. 33, *G*. At a distance of a few mm. only from the root-apex we find the epidermis dead, while the cortical layer next to the outermost one only gradually attains the wall-thickness figured, viz. about 2.5 μ. The dead epidermis does not however persist everywhere, as the figure indicates, often only fragments of the radial walls are found.

There are somewhat considerable differences in the anatomical structure of the aerial and the under-ground stem

in *Rub. chamæmorus*, differences which are connected with differences of life-duration and function. The conducting tissue exhibits the greatest differences. In the aerial shoot there are about 10 primary bundles separated by narrow medullary rays which remain in their primary condition; the intrafascicular cambium forms only a small amount of wood. I have not been able to see any endodermis in the aerial shoots, though such is distinctly seen in the wandering shoots. In the latter a continuous cambium begins to function very early and a considerable amount of wood is formed containing numerous medullary rays which are usually one cell-layer broad. In older rhizomes more or less distinct annual rings occur; the oldest I have seen were, however, only three years old. As regards the proportion between the diameter of the pith and that of the whole organ, the usual difference obtains between aerial and under-ground shoots; the proportion in the aerial shoot is larger (about $\frac{1}{2}$) than in the runners measured in their primary condition ($\frac{1}{3}$—$\frac{2}{5}$). In addition there is found in the aerial shoot, but not in the runners, a fairly thick fibrous tissue outside the phloem, and the outermost cortical layer is somewhat collenchymatous. The cortex in the runners is considerably thicker than in the aerial shoot, but more space is not thereby gained for reserve food-material, because even in the first vegetation-period of the shoot a periderm is formed in the outermost layer of the pericycle. Then the cortex collapses and persists during the following years as a loose brown mantle around the rhizome. But even in the third year the phellogen has not been able to form more than 3—4 layers of which the outer have become corky. In the aerial stem no periderm is developed, not even so much as in *Rub. arcticus* (Fig. 36, *F*); consequently, the structure of the assimilatory shoot of *Rub. chamæmorus* is the simplest among the species of *Sect. Cylactis* here investigated. — The epidermis around the young runner

has thin walls, and the protective layer described for the roots is altogether wanting.

The pith is heterogenous as in the two other species; Fig. 33, *F* shows a somewhat tangential longitudinal section through the central part of the pith of a runner. The active cells, which have somewhat stronger walls in the aerial stem than in the runners, form in addition to a continuous marginal part (of which *mp* in the figure is the innermost layer) also slightly anastomosing rows in the central part (*mc*) of the pith where the majority of the cells are dead. But notwithstanding this structure the pith is the chief depository of food-material, and during autumn is found crowded with starch; in addition, the medullary rays and the pericycle in the runners serve as reservoirs of starch.

Though *Rub. chamæmorus* is not an evergreen yet its leaves have in one respect a xeromorphous structure: the upper epidermis has mucilaginous inner walls (Fig. 33, *A*), a fact which has already been mentioned by KRUCH (l. c.). KIHLMAN (l. c., p. 113) was probably ignorant of this since he mentions, among others, *Rub. chamæmorus* and *Potentilla palustris* (which has also mucilaginous walls in the upper epidermis of the leaf) as striking examples of bog-plants without special protective devices against excessive transpiration (see p. 119). Otherwise the leaf has the usual mesophyllous structure; it is rather thin (170—190 μ) and the proportion between the thickness of the leaf and the thickness of the palisade tissue varied from about $\frac{2}{1}$ (Godthaab in Greenland) to $\frac{2.4}{1}$ (Bosekop in Arctic Norway). The outer wall of the upper epidermis is 2—2.5 μ thick and that of the lower somewhat thinner. Stomata occur only upon the lower surface; they are not definitely arranged. The radial walls in the epidermis are somewhat wavy, usually somewhat more so upon the lower than upon the upper surface. The palisade parenchyma is present in 2—3 layers and the spongy parenchyma is loose in structure. (Fig. 33, *A*, *B*, *C*, *D*).

The larger bundles are very prominent upon the lower surface of the leaf which helps to support the large reniform blade. These ribs consist not only of conducting tissue proper, but also of rather thick-walled vein-parenchyma. True stereom was not observed in the leaf. Along the veins upon both sides, but especially upon the under side, such glandular

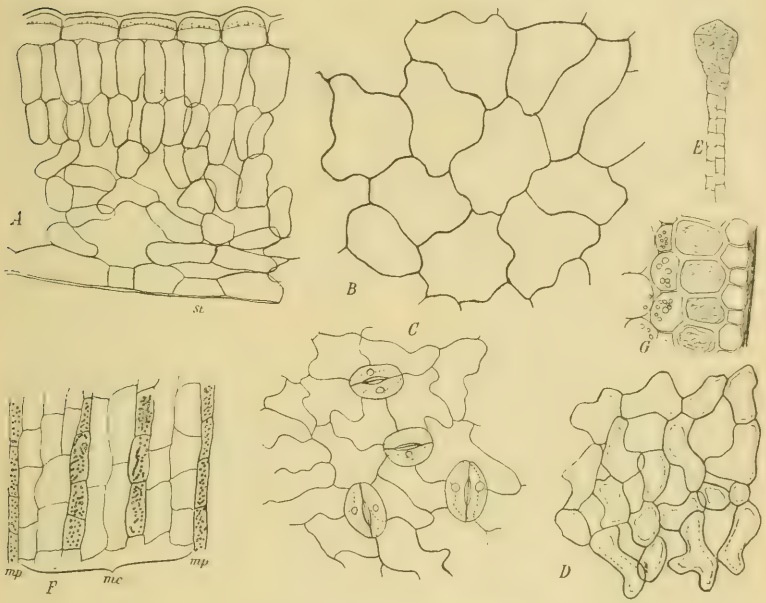

Fig. 33. *Rubus chamæmorus.*

A, Transverse section of leaf, the inner wall of the upper epidermis is mucilaginous. *B*, Epidermis of the upper surface of the leaf. *C*, Epidermis of the lower surface of the leaf. *D*, Section of the spongy parenchyma of the leaf parallel to the surface. (*A*, *B*, *C* and *D* from Greenland.) *E*, Glandular hair from the lower surface of the leaf (Norway). *F*, Longitudinal section through the central part of the pith in a runner (Denmark). *G*, The peripheral part of an absorbent root in transverse section, the epidermis has collapsed, the layer within the exodermis has strong walls (Denmark). *A*, *B*, *C*, *D*, *F* and *G* $^{200}/_{1}$; *E*,$^{90}/_{1}$.

hairs are found as shown in Fig. 33, *E;* scattered unicellular hairs of the usual appearance are also met with.

In the anatomy of the leaf-stalk *Rub. chamæmorus* differs considerably from *Rub. saxatilis* and *Rub. arcticus*, which is of interest as Fritsch has shown that a certain systematic

importance must be attached to the number of the vascular bundles and their course in the leaf-stalk of *Rubus*. And as the group *Cylactis* (Raf.) Focke in this as well as in most other points has not previously been anatomically investigated I shall give a description of the present case. With the exception of some individual variations the facts are as follows: As in all the species investigated by FRITSCH, and as in the two other species mentioned here, so also in the present species three vascular bundles enter the leaf-stalk; after a course of about one cm. the two upper divide each into two bundles, and in the whole length of the stalk up to a few mm. from the leaf-blade there are five bundles; at this level one lateral bundle on each side unites with the median one, but the latter divides again into three before the stalk passes into the leaf-blade. The bundles are stiffened by a fibrous tissue along the sieve-tissue.

As regards the structure of the flower of *Rub. Chamæmorus* WARMING says in his notes: "Both in northernmost Norway and in Greenland I found the cloud-berry to be purely dioecious and the degree of abortion of the one sex was almost the same in both places. If I may point out any differences it would be that: (1) The Greenlandic flowers are perhaps slightly smaller than the Norwegian; the diameter of the latter I have found to vary between 2½ and 3½ cm. as regards the male flowers and to be about 2½ cm. for the female flowers; the Greenlandic were 2—2½ cm. for both kinds of flowers, but the material in hand was extremely sparse. (2) The Greenlandic appear to have slightly less rudimentary stamens in the female flowers and likewise slightly less rudimentary pistils in the male flowers than have the Norwegian. In the former the stamens had a somewhat larger anther, in the latter the carpel was more highly developed and the ovule was even indicated, as the figures show." . . . . "As regards the flower it may be added,

that it is 4—6-merous in calyx and corolla, sometimes purely so, but sometimes with one or other sepal broader than the rest and cleft, a transitional stage to becoming two. In some flowers the hypanthium is quite smooth in the interior, in others it is, over the greater part of the surface or only at the bottom, covered with long, stiff, thick-walled hairs which are quite smooth exteriorly. In the male flowers many pollen-grains were found between these hairs and between the pistil-rudiments."

In 1887 LINDMAN recorded *Rub. chamæmorus* from

Fig. 34. *Rubus chamæmorus.*

A, Male flower from Arctic Norway; June 25 ($^2/_1$). *B*, Female flower from Greenland ($^4/_1$). *C*, Carpel of a male flower from Arctic Norway, in the hollow a slight indication of the ovule is seen ($^{45}/_1$). *D*, The somewhat folded and slightly lobed stigma of a female flower from Arctic Norway (about $^{50}/_1$). Drawn by Eug. Warming.

Dovre (Scandinavia). He found only unisexual flowers with very small rudiments of the other sex. In the female flowers the petals were 8—10 mm., in the male flowers about 15 mm. long. AXELL[1] (pp. 46—48, Fig. 11, *a*, *b*) records *Rub. chamæm.* as trioecious-polygamous (quoted after LINDMAN). In 1903 POPPIUS mentions *Rub. chamæm.* In the female flowers he finds slight or no secretion of honey; in the male flowers honey

[1] Om Anordningarne för de fanerog. växternas befruktning. 1869.

is secreted more abundantly, the stamens are well-developed, with brown anthers, the carpels are very rudimentary and scarcely visible in the hypanthium. Insect-visitors to the flowers are fairly frequent, especially flies. In the male flowers they devour partly honey and partly pollen, in the female flowers it is probably the white stamen-rudiments which attract them, because their attention is always drawn to these staminodes.

In Spitzbergen the plant has been collected with flowers twice only; the second time numerous flowers were found at Kol Bay (23 . 7 . 1898); they were smaller than those from the district of Tromsö (Arctic Norway) and were all female (ANDERSS. and HESSELM.).

In Greenland it is peculiar that the two sexes have not been found in the same locality. Thus, only male flowers have been found at Julianehaab and on the large island to the west of Ameralikfjord, while only female flowers have been gathered in different localities near Godthaab (VAHL [see WARMING, 1886], LANGE, ROSENVINGE and HARTZ). WARMING (l. c.) mentions that WORMSKJOLD records fruit of *Rub. Chamæmorus* from Greenland, and ROSENVINGE (l. c.) says that it appears to set ripe fruit at Kasigiànguit near Godthaab. Otherwise it is not known to bear fruit in Greenland. As regards this point NORMAN records from Arctic Norway that it sets fruit there in favourable years, even in the northernmost districts; in the highest habitats it never flowers, and A. CLEVE (loc. cit., p. 47) records that it is often sterile in the mountains of northern Sweden. In places on the coast of Arctic Norway, at higher levels above the sea, it bears almost exclusively male flowers and probably every year; and NORMAN says that in certain years, only or almost only male flowers occur over very large areas so that the harvest fails entirely. Lastly, POPPIUS (l. c.) mentions the distribution of the two sexes;

he found that at Esbo in Finland the female flowers which were somewhat more numerous than the male, usually occurred in more open places in the marshes and bogs, while on the other hand the male flowers were somewhat more numerous in shady localities.

Flowering begins in June (Lange, Norman). In Arctic Norway birds are important agents in fruit-dispersal; and bears probably also play a part in this connection (Norman).

Rubus arcticus L.

Lit. Trecul, 1865. Warming, 1886, b. Norman 1895. Poppius, 1903. Sylvén, 1906.

This species is found in the whole of the Subarctic zone, and extends but rarely into the Arctic, namely in Norway, where its northern limit lies somewhat to the south of 71°. Norman writes that it thrives both in dry and damp localities and even in bogs, where it occurs especially on knolls.

The alcohol material was collected in northern Scandinavia.

Rubus arcticus does not develop wandering shoots, but vegetative propagation is effected by bud-producing roots; Warming (1886) records this from Bosekop in Arctic Norway: "Its (*Rub. arct.*) unbranched or slightly branching shoot, which is a few inches high, occurred always singly but socially over larger or smaller patches of the field" and "it was proved that this species was chiefly propagated by root-shoots, consequently it has shoots of the same structure as have those of a great many similar plants, e. g. *Cirsium arvense*, *Sonchus arvensis*, *Pyrola uniflora*, etc. Its shoots have elongated internodes without rosette-leaves at the base; remains of it may keep alive through the winter and next spring produce a new shoot as the figure (Fig. 35, *A*) shows." A sympodium is thus formed which may include at least four shoot-generations. These root-shoots sometimes go through a stage of

growth in vigour before they flower, but I have not been able to investigate such shoots in the material at my disposal, therefore I shall only deal with the propagative shoots formed by the stems.

In correlation with the fact that vegetative propagation

Fig. 35. *Rubus arcticus.*

A, Portion of root with a shoot-complex arising from it. The first leaf of the lateral shoots is marked with a × (Arctic Norway, July, 1885; $^1/_1$); drawn by Eug. Warming (l. c.). *B*, A plant which had been growing in a sphagnum-bog in the province of Quebec in Canada, Aug., 1907; *l*, the stalk of a foliage-leaf; *s*, propagating shoot; (slightly above nat. size); drawn from a specimen in the Botanical Museum in Copenhagen.

is effected by the roots, the plant has one kind of shoot only, viz. assimilatory floral-shoots which have a two years development. In the first year an erectly ascending, and when the plant is growing in dry soil, short propagating shoot is

formed, which usually bears 4—6 scale-leaves in two rows; it probably does not elongate until the end of summer. The specimens figured in Fig. 35, *B* had been growing in a sphagnum-bog, and the height of the latter has compelled the young shoot to elongate to an unusual extent. The propagative shoots pass through the winter with their apices at the surface of the ground. Next year the assimilatory shoot is formed, which also has elongated internodes; it is terminated by the solitary flower or by the dead apex of the stem which is hidden in the upper leaf-sheath. The foliage-leaves, which are usually few in number, are two-rowed as are the scale-leaves. Often, the foliage-leaves, especially the upper, also subtend solitary flowers, or slender vegetative shoots occur. The propagating shoots, two or more of which may occur, are as a rule subtended by the lower scale-leaves; buds subtended by other scale-leaves remain dormant or the upper ones may develop proleptically during the same year as the parent-shoot, which results in the individuals becoming fairly rich in shoots. — According to Sylvén *Rub. arcticus* appears to pass through the winter in a partially green condition.

Anatomy. The horizontal shoot-bearing roots are protected by a cork-periderm of about 6 layers without intercellular spaces. They are in connection with the shoot-bases, the plant's reservoir of food-material, and in them the several-layered pericycle and the one-layered, but several cells high, medullary rays in the secondary wood become filled with starch. From the rhizome adventitious roots arise. The absorbent roots are of the nature of mycorrhiza and have a peculiar structure. The epidermis consists of low cells with very strong outer walls (4 μ thick). The structure of the inner layer of the cortex, which is about 4 layers thick, is as in *Rub. saxatilis*, but the thickenings of the walls are less and there is an unthickened part on the outer tangential wall. The rather thick endodermis, the thickenings of the

walls mentioned above, and the epidermis turned yellow when treated with chloride-zinc-iodine. (Fig. 36, *E*).

The anatomical structure of the annual aerial shoot is naturally very different from that of the perennial rhizome. In the latter secondary wood is developed which forms annual rings, and the primary cortex is thrown off, a periderm of about 6 layers without intercellular spaces and consisting chiefly of cork being formed in the pericycle. The latter, a few layers of phelloid-cells, the medullary rays, which are of the same structure as those of the root, and especially the peripheral part of the pith are depositories for starch. The aerial shoot remains in a far higher degree in the primary condition. A continuous cambium in the lower part forms only a small quantity of wood, and it is likewise only in the lower portion that a periderm is found like that shown in Fig. 36, *F*. In the cortical layer bordering on the bast-ring tangential walls are developed, the walls in the outer layer thereby formed become corky, but the inner layer which corresponds to the phellogen remains unaltered. This rudimentary periderm distinguishes with certainty the stem of *Rub. arcticus* from that of *Rub. Chamæmorus*. — The bast, which is absent from the rhizome, is about 3 layers thick in the lower part of the stem and forms a continuous ring, becoming weaker upwards. Endodermis is absent, but is present in the perennial part of the stem. The outer wall of the epidermis is rather thick and has a well-developed cuticle. Within the epidermis there are two layers of slightly developed collenchyma. — The pith has the usual peripheral layer of starch-containing cells, but in the central part I have seen no such cells. TRECUL (l. c.) who has described the pith records that in the central part a few isolated cells were found containing tannin.

The leaf, which probably as a rule lives one summer only (see p. 93), has the usual mesophyllous structure;

it bears on both sides, especially on the veins, scattered unicellular hairs. The outer wall of the upper epidermis is about 2.5 μ thick. The stomata occur only upon the lower surface and are on a level with the surface. Palisade parenchyma occurs in 1—3 layers. The proportion between the leaf-thickness (about: 155 μ) and the thickness of the palisade tissue was about $\frac{2}{1}$. The spongy parenchyma is loose. Fig. 36, *A*, *B*, *C*, *D*.

The structure of the leaf-stalk is as in *Rub. saxatilis;*

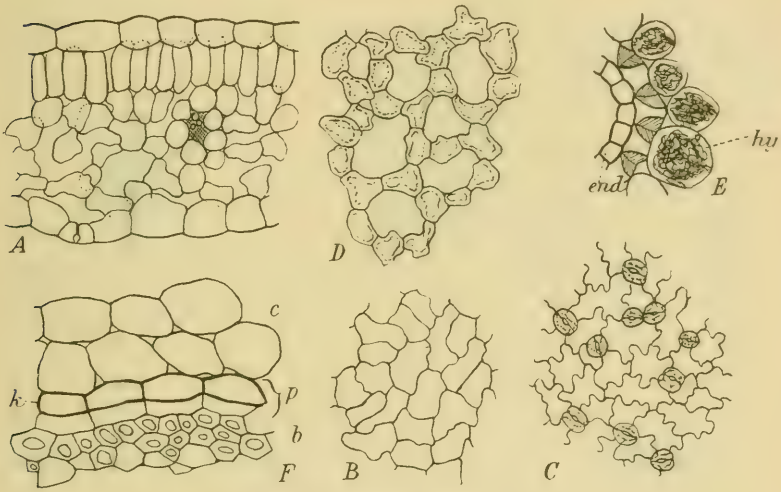

Fig. 36. *Rubus arcticus.*

A. Transverse section of leaf. *B*, Epidermis of upper surface. *C*, Epidermis of lower surface. *D*, Section of spongy parenchyma parallel to the surface. *E*, Portion of a transverse section through an absorbent root; *end*, endodermis; *hy*, fungal hyphae, the innermost layer of the cortex has highly thickened radical walls. *F*, Portion of a transverse section through an aerial stem; *b*, the bast outside the leptome; *c*, cortical cells; *k*, the cork-layer in the rudimentary periderm *p*. *A*, *B*, *C*, *D*, *E* from Bosekop and *F* from Ångermanland in Sweden. (*A*, *D* $^{190}/_{1}$; *B*, *C* $^{140}/_{1}$; *E*, *F* $^{314}/_{1}$).

along the greater part of the length of the stalk there are three bundles, and only along a very short distance, immediately after the three bundles have emerged from the stem there are 5 bundles. The stereom is very much as in *Rub. saxatilis.*

The flower-biology was first treated by Warming

(1886), who says: "The hermaphrodite flowers are 6- or 7-merous, more rarely 8-merous and have a varying diameter (about 18—30 mm.). The dark-crimson, stellately expanded or even somewhat reflexed petals are highly conspicuous with the green field as a background; therefore it is interesting that the flower is nevertheless well adapted for self-pollination."

"On regarding the flower from above one does not see, as in the other *Rubus*-species, that the styles with the stigmas

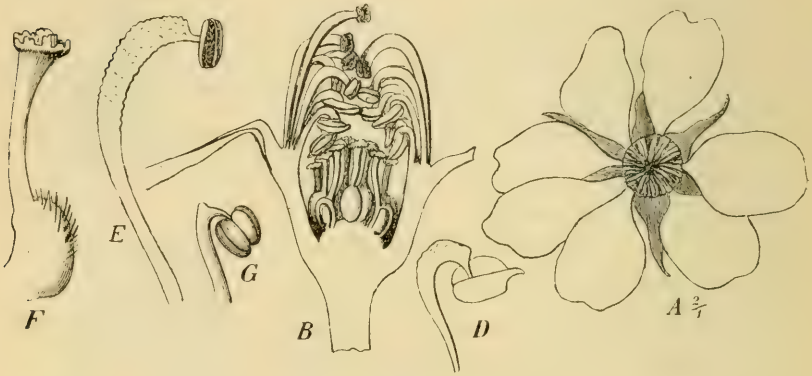

Fig. 37. *Rubus arcticus.*

A, A flower seen from above. *B*, A longitudinal section through a flower the anthers of the outermost stamens have opened. *D* and *G*, Two stamens from the innermost circle. *E*, A stamen from the outermost circle. *F*, A pistil. — Cf. text. *D*, *E*, *F* *G* $^{10}/_{1}$; Arctic Norway. (Eug. Warming l. c.)

are situated in the middle and are closely surrounded by the stamens, which are of about the same length; here, only the stamens are seen which from all sides bend inwards toward the centre of the flower so that the central part is quite hidden. A longitudinal section shows best how they unite closely in a conical fashion with the upper ends more or less bent inwards and with all the anthers gathered above the centre of the flower. (Fig. 37, *A*, *B*). The outermost stamens are the longest, their filaments become, from a thinner, entirely smooth base, gradually thicker and also covered with small

warts. Immediately below the anther the filament becomes suddenly thinner. The nearer the stamens approach the centre of the flower, the smaller they are and the more bent inwards; the smallest of all have short much bent filaments the upper thinner part of which is however as long or even longer than that of the outermost stamens (Fig. 37, *D*, *G*). As the stamens are so densely and closely united above the centre of the flower it appears as if all smaller and weaker insects must be entirely excluded from access to the honey secreted by the inner side of the hypanthium. I think that only strong insects such as humble-bees and bees will be able to force a way, but perhaps the slender proboscis of the butterfly may discover a way down between the filaments."

"Longitudinal sections show moreover that the pistils are lying hidden just below the stamens. The styles, which are slightly thickened towards the apices, are erect, and the irregularly lobed stigmas (Fig. 37, *F*) are thereby placed immediately below the anthers, and partially even in direct contact with those of the innermost, short stamens. The flowers are slightly protandrous; the outermost stamens open their anthers very early even at the time when the petals still stand almost erect, and before the stigmas are quite mature, though large. But the stigmas evidently become functional very quickly after the outermost stamens, because I have seen the stigmas covered with quantities of germinated pollen before the anthers of the innermost stamens have opened. Cross-pollination must be possible: but I also believe that pollen must almost certainly fall from the anthers of a flower upon its own stigmas, when an insect thrusts its proboscis down between the stamens, and this evidently happens the more easily because the filaments are rough and must therefore offer more resistance to the intruding proboscis of an insect, and thus be shaken so much more effectively. It will then depend on whether the pollen

from the flower of another individual germinates or develops more quickly than does the pollen of the same flower. But in case cross-pollination does not take place, self-pollination is inevitable ultimately when the short stamens dehisce."

"I know no other *Rubus*-species in which self-pollination is so well secured as in the present species, and this must undoubtedly be regarded as an adaptation of the species to the inclemency of the weather, to which it is probably often exposed during its flowering period. The species which comes nearest to it is, according to my observations, *Rubus saxatilis*, which as is well-known extends even to the North Cape and East Finmark and above the wood-limit in the mountains of Norway and in the Alps."

POPPIUS (l. c.) finds that the flowers are without scent and secrete very little honey; he also records a proterandrous stage before the homogamous. He writes that in foggy or overcast weather the stamens bend inwards so that the anthers and filaments entirely cover the pistils. Numerous insect-visitors are mentioned. NORMAN records that in the districts of Arctic Norway where the plant sets fruit rarely or only sparingly, the corolla is largest and most showy, frequently with 6—8 petals which are 13—14 mm. long and 8—10 mm. broad, while in districts where the plant bears fruit frequently the corolla is often much smaller, with petals the length of which may be reduced to 9 mm. and breadth to 5.5 mm. In Arctic Norway *Rub. arcticus* flowers in the end of June and has ripe fruit in August (NORMAN). — Fruit-dispersal probably by birds.

According to the microscopical investigation of *Rubus chamæmorus*, *Rub. saxatilis* and *Rub. arcticus* mentioned above, the first-named differs in several points from the other two, viz. (1) in the structure of the absorbent roots, (2) in the structure of the aerial shoot, (3) by the fact of its leaves bearing stalked

glands and having mucilaginous inner-walls in the epidermis of the upper side, and lastly (4) in the number of the vascular bundles in the leaf-stalk, where *Rub. chamæmorus* has five and the others three. According to Fritsch (l. c.) special importance should be attached to the last feature when the question is to distinguish anatomically species and groups of species among the *Rubi*. Thus, the anatomical investigation together with the morphological appears to support Focke[1] who separates *Rub. chamæmorus* from the other herbaceous *Rubi* and places it in a distinct subgenus.

Alchimilla alpina L and **A. færoensis** (Lge) Buser.

Lit. Müller, 1881. Jónsson, 1895. Norman, 1895. Knothe, 1902. Schrøter, 1904. Hollstein, 1907.

As these two species agree in many of the points which have been investigated they are here treated jointly for brevity's sake.

A. alpina extends north of the Polar circle in Scandinavia only; it is found also in Greenland, Iceland, the Færöes, the mountains of Central Europe and in the Urals. *A. færoensis* has been found only in the Færöes and in Iceland. The habitats are more or less dry, but *A. alpina* at any rate can live in widely different conditions: in grassy localities, on cliffs, on heaths, rocky flats, in willow copses, etc.

The alcohol material was gathered in Greenland, Iceland and the Færøes.

A. alpina has a primary root of rather long duration from which the shoots spread out upon the ground with apices turned upwards. Usually the shoots do not reach any considerable length; they branch freely and are fixed to the ground by adventitious roots. Looser or denser tufts are formed. The rhizome in *A. færoensis* is thicker than that in *A. alpina;*

[1] Abh. d. Naturw. Ver. Bremen, IV, 1874 and Synopsis Ruborum Germaniæ. Bremen, 1877.

it is vertical or obliquely ascending, branches less freely, and the branches are considerably shorter, but they develop adventitious roots as in *A. alpina*. Undoubtedly, neither species is entirely dependent on the primary root for the continuation of life; vegetative propagation takes place. Fragments of the dead leaves persist for a longer time, but in *A. alpina* at least the shoots may ultimately get rid of them.

The leaves are placed in a rosette, but in luxuriant specimens of *A. alpina* the internodes may be somewhat elongated. The first leaf of the shoots — both of the floral and the vegetative — is a scale-leaf in the form of a closed sheath; also the other leaves have closed sheaths which are ruptured on the vegetative shoots owing to growth in thickness. In Iceland JÓNSSON found *A. alpina* with green leaves in the winter. The old leaves had not fallen off, but formed a sort of waterproof roof over the shoots (l. c.). In the Botanic Garden in Copenhagen the leaves which remain green through the winter are, in both the species, very small, few in number and not quite expanded. The summer-leaves wither in the autumn and a few new leaves may grow out, but strictly speaking the plant is scarcely winter-green. The shoot-apices are protected by the closely folding leaf-sheaths; scale-leaves are not developed.

In the Botanic Garden in Copenhagen there is no fixed flowering-period, but new floral shoots are constantly being developed as in the *A. vulgaris*-forms, though not to the same extent as in the latter; and not until the low temperature of winter sets in does the development cease. In December all transitional forms are found, from flowering shoots to quite young buds which are hidden by the leaf-sheaths of the terminal bud. I am not prepared to state whether a similar proleptic development takes place in Arctic Norway and in Greenland. NORMAN and LANGE record that the flowering in these regions ends on September 20 and in August

respectively. In Iceland Jónsson (l. c.) found no flower-buds on March 26, but, as Fig. 38, *A* shows, young inflorescences are at any rate to be found in Greenland in August.

Anatomy. The adventitious roots are triarch-tetrarch. The central cylinder is surrounded by a suberized endodermis. The outer wall of the epidermis, especially in *A. alpina*, is somewhat thick (2.5 μ), but the skin is functional for a certain period only, after which it is thrown off; this is due to a structural feature which is shown in Fig. 38, *B* and which was especially pronounced in *A. færøensis*. The exodermis consists of large cells, the thin radial walls of which are ruptured sooner

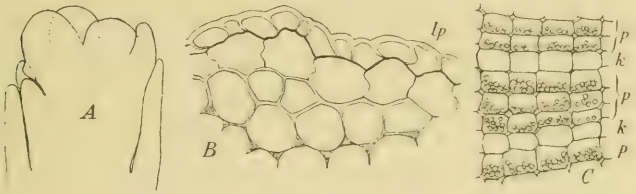

Fig. 38.

Alchimilla alpina: A, Longitudinal section through a young bud containing the primordium of an inflorescence (Greenland; 1. 8. 1885; $^1/_{60}$). *C*, Portion of a transverse section through the periderm of a rhizome (Greenland; $^{175}/_1$); *k*, layer of cork; *p*, phelloid-cells. — *Alchimilla færøensis: B*, Portion of a transverse section of a young adventitious root of the first order; *lp*, epidermis ($^{240}/_1$).

or later, and the following layer of the cortex which has fairly thick walls and gradually becomes corky, functions then as epidermis till the periderm is formed. The primary epidermis is thrown off before the root in the zone in question has begun its secondary growth in thickness.

In the primary cortex in the roots of *A. alpina* fungal hyphæ have been found.

Periderm is probably formed in the pericycle; it is not developed until a continuous woody portion is produced in the central cylinder; it consists of alternating series of layers of 1—3 layers of cork-cells and phelloid-cells; it contains rather large intercellular spaces which are however often absent

from the inner side of the cork-layers. The phelloid-cells contain starch-grains which are found especially along the inner walls. The periderm may constitute as much as $\frac{1}{5}$ of the radius of the root. Medullary rays are absent from the wood. There are distinct annual rings; the oldest roots I have seen were 5 years.

The central cylinder in the rhizome is surrounded by a distinct endodermis. The primary bundles are considerable in number and are more or less confluent. The pith which is of simple parenchyma lives in *A. alpina* as long as the shoot, but in *A. færøensis* it apparently dies at an earlier period. In the latter species the pith constitutes a larger portion of the diameter of the shoot than in the former; it is the chief reservoir of food-material and in the autumn is found crowded with starch. Rhizomes of *A. alpina* collected in Iceland in March contained, on the other hand, almost no starch, and shoots of both species collected in the Botanic Garden in Copenhagen on Jan. 5 contained only a small quantity; on the other hand, they contained large quantities of fat.

In the first period of vegetation of the shoot a continuous cambium produces a small quantity of wood. Medullary rays are absent from the latter (cf. HOLLSTEIN who has studied *A. alpina*). In *A. alpina* the diameter of the vessels was larger in specimens from Copenhagen than in those from more northern regions.

The periderm is formed by the division of the outermost layer of the pericycle and is developed even in the first period of vegetation of the shoot. 2—3 layers of phelloid-cells alternate with one layer of cork-cells. But in the Botanic Garden in Copenhagen the periderm in these two species contained only scattered cork-cells; in such plants it functions almost solely as a depository of food-material while the protective layer proper consists of dead masses of leaf-sheaths, primary cortex and the older layer of the periderm.

Fig. 38, *C* shows a transverse section of the periderm of *A. alpina;* it contains large intercellular spaces. During summer the starch-grains are found especially along the inner walls of the phelloid-cells; in the autumn the cells are entirely filled by them.

The primary cortex is ruptured owing to secondary formations, but even in the second summer it may be found alive. Bast does not occur.

The structure of the floral-shoot is very much like that described by Hollstein from the Dauphiné-Alps. A collenchyma, 1—2 layers thick, occurs, and within the endodermis 2—3 layers of bast unite with the secondary wood, which consists of several-layered strong-walled tracheids, so that the groups of sieve-tissue are entirely surrounded by stereom. The pith dies away in the centre.

The leaves are from 200 to 220 μ thick, and generally somewhat thicker in *A. alpina* than in *A. færoensis.* The epidermis of the upper surface is glabrous in the former and slightly hairy in the latter; it is high, and the outer wall in *A. alpina* is about 6 μ and in *A. færoensis* 4—5 μ thick, while the outer wall in the epidermis of the lower surface is about 3.3 μ and about 2 μ thick respectively. Stomata serving as respiratory organs are absent from the upper surface. The lower surface is densely hairy and here the stomata occur abundantly and are somewhat sunk below the level of the surface (Fig. 39, *B*). Knothe (l. c.) illustrates by a figure of *A. alpina* how the hairs are appressed upon the lower surface of the leaf, and he states that this is not wetted. The palisade parenchyma consists of a well-marked layer which constitutes about one-half of the thickness of the mesophyll. The proportion between the leaf-thickness and the thickness of the palisade tissue is in *A. alpina* about $\frac{2}{1}$ and in *A. færoensis* about $\frac{2.4}{1}$. The intercellular spaces in the spongy parenchyma are not large, but sections

often show large slit-like lacunæ on the dorsal side of the leaf. Stereom is absent from the leaves. Fig. 39 (*A*, *B*, *C*, *D*, *E*).

At the apex of the leaf-teeth there is a slightly developed epithema, below which tracheids terminate; water-stomata occur upon the upper surface of the leaf-teeth on a limited area.

The three bundles in the leaf-stalks of these two

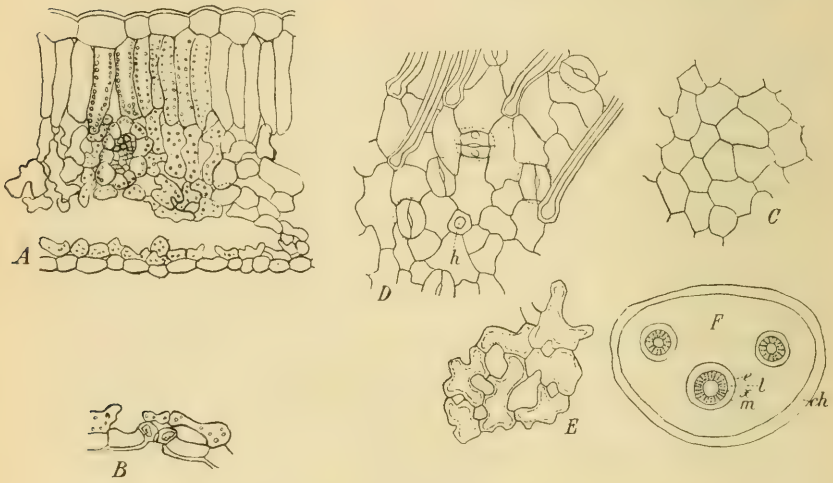

Fig. 39.

Alchimilla alpina from Greenland. *A*, Transverse section of leaf ($^{160}/_{1}$). *B*, Stoma ($^{200}/_{1}$). *C*, Epidermis of the upper surface of the leaf ($^{100}/_{1}$). *D*, Epidermis of the lower surface of the leaf with hairs and stomata ($^{200}/_{1}$). *E*, Section of spongy parenchyma parallel to the surface ($^{200}/_{1}$). — *Alchimilla fœroensis*. *F*, Transverse section of leaf-stalk ($^{20}/_{1}$); *ch*, collenchyma; *e*, endodermis; *l*, leptome; *x*, xylem; *m*, "pith".

species are concentric in structure. This peculiar feature was first demonstrated by C. de CANDOLLE[1] in a great many *Alchimilla*-species, among others also in *A. alpina* and *A. minor*, and afterwards BOUYGUES[2], without mentioning de CANDOLLE's paper, has published a short note upon the same subject. BUSER[3] has been studying de CANDOLLE's

[1] Bull. de l'herbier Boissier, T. I, 1893.
[2] Act. soc. Linn. de Bordèaux, 1900.
[3] Bull. de l'herbier Boissier, T. II, 1894.

results and shows that the species which have the concentric structure of the bundles of the leaf-stalk are found in the "region montagneuse" of the Alps, while the subnival Alpine species have the common collateral structure of the bundles. Fig. 39, *F* shows a transverse section of the stalk of *A. færoensis*.

As is well-known S. Murbeck[1] has demonstrated parthenogeny in a whole series of *Alchimilla*-species including *A. alpina* in which development of the embryo frequently takes place even while the flower is in the bud-condition. Murbeck did not find a single pollen-grain capable of germination in *A. alpina*. Nor does *A. færoensis* appear to develop pollen-grains capable of germination.

In the insignificant yellowish-green, apetalous flowers there is around the gynaeceum a broad fleshy disk which secretes honey. H. Müller (l. c.) has described the structure of the flower of *A. alpina*.

Alchimilla vulgaris L.

Lit. H. Müller, 1881. Leist, 1889. Jónsson, 1895. Norman, 1895. Sylvén, 1906.

In Arctic Norway this collective species grows in widely different localities, having been found both in dry and in damp places, in open spots and in birch-woods (Norman). In Greenland it grows in damp grassy fields and in willow-copses.

In my material the following elementary species occurred: *A. acutidens* Bus., *glomerulans* Bus., and *minor* Huds. All these species extend to the north of the Polar circle in Greenland and Europe; they are also found in Iceland, and *A. acutidens* and *A. minor* occur in the Færoes; they are found, in

[1] Parthenogen. Embryobild. in d. Gattung *Alchimilla*. Act. Univer. Lundensis T. 36, 2.

addition, in northern temperate Europe[1]. — The alcohol material is from Greenland, Iceland and the Færøes.

The young seedling of *A. vulgaris* is according to SYLVÉN a rosette, and in older plants also the leaves are always placed in a rosette even if the internodes are often somewhat elongated. The rhizome is vertical or oblique or almost horizontal, and in the last case there may be a slight wandering. It does not branch so freely as in *A. alpina.* Even during the year in which it germinates adventitious roots arise, and these are afterwards developed abundantly.

The floral axes are lateral, and there occurs, at any rate in several of the elementary species growing in Denmark, a similar proleptic development of the floral shoots as in *A. alpina* in Copenhagen, only the development is more vigorous. It appears to be external factors (e. g. fall of temperature) rather than internal which limit the flowering period; we may be justified in presuming that something similar happens also in the Arctic regions; NORMAN records that in Arctic Norway *A. vulgaris* may flower till September 20.

The plant lives through the winter in a more or less green condition (WARMING, 1884; JÓNSSON and SYLVÉN); but we may also find it without any green leaves (in Denmark) and as in *A. alpina* the summer leaves wither in the autumn. The shoot-apex is protected by the sheaths of the foliage-leaves; scale-leaves are not developed.

Anatomy. — Roots of *A. minor* and *A. acutidens* have been investigated; in structure they resemble essentially those of *A. alpina* and *A. færoensis* (cf. Fig. 38, *B*). Mycorrhiza has been found in *A. acutidens* from Iceland.

The rhizomes are on an average thicker than those of *A. alpina;* this is especially due to the fact that the pith is

[1] See Harald Lindberg. Die nordischen *Alchimilla vulgaris*-Formen und ihre Verbreitung. Acta Soc. Scient. Fenn. XXXVII. Helsingfors, 1909.

largely developed. Otherwise, the structure of both the rhizomes and the stems is practically similar to that in *A. alpina* and *A. færøensis*.

The anatomy of the leaves (Fig. 40) is the same in all these three species, and closely resembles that of the two species mentioned above; the leaves are, however, somewhat more mesomorphic than those in *A. alpina*. The upper surface of the leaf is glabrous, or in *A. glomerulans* slightly hairy, the lower surface is slightly hairy. The outer wall of the epidermis

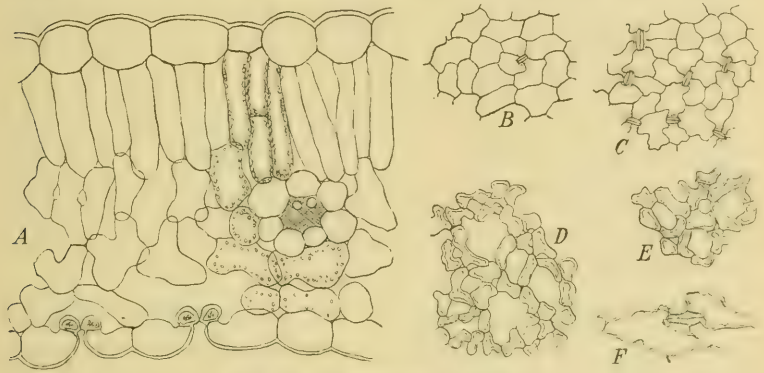

Fig. 40. *Alchimilla vulgaris*.

A. glomerulans. *A*, Transverse section of leaf. *C*, Epidermis of the lower surface of the leaf. *E*, Section of spongy parenchyma parallel to the surface. — *A. minor*. *B*. Epidermis of the upper surface of the leaf. *D*, Section of spongy parenchyma parallel to the surface. — *A. acutidens*. *F*, Stoma from the epidermis of the lower surface of the leaf (*A*, about $^{220}/_{1}$; *B*, *C*, *D* and *E*, about $^{100}/_{1}$; *F*, about $^{150}/_{1}$; *A*, *C* and *E* from West Greenland, *B* and *D* from Dr. Louises O in East Greenland, *F* from Eskefjord in East Iceland).

of the upper surface is about 2 μ thick; the radial walls are slightly undulating. Stomata occur scattered upon the upper surface and, as upon the lower, they are situated below the level of the surface and on an average somewhat more so than is the case in the two species of the *Alpina*-group (Fig. 40 *A*). The radial walls of the lower epidermis are somewhat more strongly undulating than those of the upper. A layer of well-marked palisade-cells occur and sometimes another layer consisting of more irregularly formed cells. Leist records only one layer of palisade-cells. The proportion between the leaf-

thickness (about 190 μ) and the thickness of the palisade-tissue is about $\frac{2}{1}$. Below the stomata of the upper surface air-spaces are produced in the same manner as described for *Sibbaldia procumbens* (p. 58). The spongy parenchyma is rather loose in structure and contains, as shown in Fig. 40, *D*, besides large intercellular spaces numerous very small ones. The cells are branched.

The leaf-teeth contain a slightly developed epithema; the water-pores occur on a limited space upon the upper surface; these structures have been mentioned by REINKE[1].

The structure of the leaf-stalk is as in *A. færøensis* and *A. alpina* (see Fig. 39, F).

MURBECK has demonstrated parthenogeny in *A. minor*, which produces only a very small quantity of imperfect pollen. — In the flowers of *A. glomerulans* from Greenland a great many of the anthers had fallen off; in those which were still attached I found no fully developed pollen.

The flowers of *A. vulgaris*, which in structure almost agree with those of *A. alpina*, have been described and figured by H. MÜLLER 1873[2] and 1881 (l. c.).

Sorbus americana Willd.

Lit. WARMING, 1887. ROSENVINGE, 1896.

The alcohol material is from Ivigtut in Greenland.

This *Sorbus* which bears much resemblance to *S. aucuparia* is a small tree with an erect, straight growth; it does not branch much, but several stems may proceed from the same root. The largest trees hitherto found in Greenland measured about 4 metres in height and the stems were about 9 cm. thick. These trees were 56 years old (ROSENVINGE). Generally, however, it is lower in growth. It occurs in south-

[1] Secretionsorg. Pringsheim Jahrb. Bd. X. 1876.
[2] Die Befruchtung der Blumen durch Insekten. Leipzig.

ern Greenland, in the valleys within the fjords, dispersed through *Betula* and *Salix* copses; it grows also in N. America.

The leaves are smooth. The epidermis shows strong cuticular stripes, strongest upon the upper surface, and upon the lower surface stronger along the margins (Fig. 41, *A*, *C*, *D*). The outer wall of the upper epidermis is about 4.5 μ

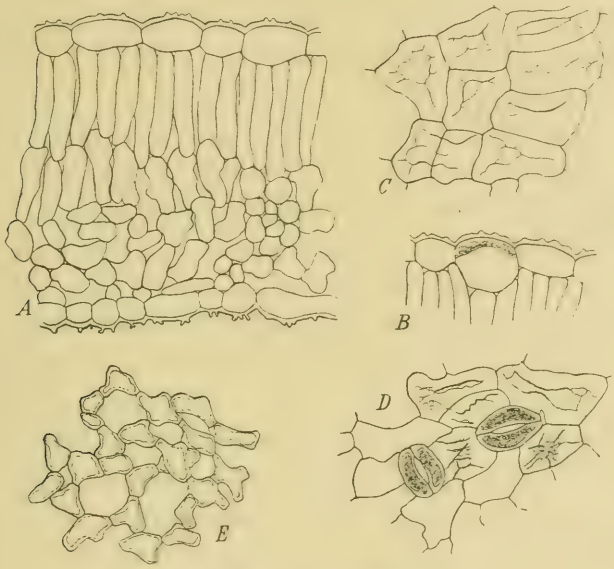

Fig. 41. *Sorbus americana.*

A, Transverse section of the leaf. *B*, Transverse section of the epidermis of the upper surface showing a cell with highly mucilaginous inner wall. *C*, Surface view of the upper epidermis of the leaf. *D*, Section parallel to the surface of the lower epidermis of the leaf; the cuticular folds of some of the cells are shown as in *C*, usually each epidermal cell has its own system of folds. *E*, Section of the spongy parenchyma of the leaf parallel to the surface. — *A*, *B*. *C*, *D*, *E* $^{185}/_{1}$. Ivigtut in Greenland.

thick, of the lower about 2.5 μ. Some of the cells in the upper epidermis have highly mucilaginous inner walls, and such cells are often particularly large (Fig. 41, *B*), compare p. 57. Stomata occur, with the exception of the water-stomata on the leaf-teeth, only on the lower surface; they are on a level with the surface. There are two layers of palisade-tissue of

which the upper consists of high, narrow cells which enclose large intercellular spaces. The cells in the second layer are often very irregular; this layer is absent above the smaller bundles in the marginal portion of the leaf. The proportion between the leaf-thickness (about 220 μ) and the thickness of the palisade tissue is about $\frac{2}{1}$. Above the larger bundles the assimilatory tissue is replaced by vein-parenchyma. The spongy parenchyma is very loose in structure, the cells are slightly or shortly stellately branched (Fig. 41, *E*).

In the flower of *Sorbus americana* I have found about 15 stamens, of which the ten episepalous were only a little taller than the five epipetalous. In *Sorbus aucuparia* there are twenty stamens[1]. — In flower-buds which are on the point of opening the stamens are found to be bent inwards over the 2—3 styles. The anthers are closed, but the stigmas are highly papillose and apparently ready to receive the pollen. When the flowers expand the stamens gradually straighten and bend outwards towards the petals. I have not found open anthers which were in contact with the stigmas, but they are seen to be bending over the latter some time after they have dehisced, and the pollen must almost certainly fall upon the stigmas. In this homogamous stage the stigmas were found to be covered with germinating pollen.

In Greenland the flowering period occurs in July and August, but according to LANGE the plant does not flower at higher altitudes. ROSENVINGE thinks that the rowan sets fruit regularly in favourable localities, and he gives some instances of its having probably been dispersed by the agency of birds.

[1] Cf. fig. 422 in Eug. Warming: Froplanterne (Spermatofyter), København, 1912.

Summary.

A. Account of the growth-form of the species.

I. Microphanerophyte: *Sorbus americana.*

Tree, low in growth. Lives through the winter without green leaves; the shoot-apex is covered by smooth bud-scales. The leaf-structure is mesomorphic.

II. Chamæphytes: *Dryas octopetala* and *D. integrifolia.*

Dwarf shrubs with a primary root of long duration. The prostrate long shoots can be somewhat individualized. In autumn the leaves die with the exception of a few half-unfolded ones at the shoot-apices. The apex of the shoot is covered by the sheaths of the young and dead foliage-leaves. The leaf-structure is xeromorphic.

III. Hemicryptophytes:

a. Dwarf shrubs or undershrubs.

Potentilla palustris is a dwarf shrub (see p. 9) which may be a hemicryptophyte, a chamæphyte[1] or a helophyte. The shoots with elongated internodes live through the winter without green leaves and with their apices covered by the sheaths of the foliage-leaves and by scale-leaves. Much wandering takes place, as also vegetative propagation. The leaf-structure is slightly xeromorphic.

Pot. tridentata is a creeping rosette-forming undershrub. Some of the summer-leaves may live through the winter; there is no closed winter-bud. The leaf-structure is xeromorphic.

[1] See also Vahl, Growth-forms of some Plant Formations of Swedish Lapland. Dansk bot. Arkiv, Bd. I, No. 2, Köbenhavn, 1913.

These two species have terminal floral-shoots while all the other *Potentillas* mentioned in this paper are monopodial.

b. Perennial herbs.

1. Spotbound are *Potentilla pulchella*, *Pot. nivea*, *Pot. Vahliana*, *Pot. emarginata*, *Pot. maculata*, *Sibbaldia procumbens*, *Alchimilla alpina*, *A. fœroensis* and *A. vulgaris*. Features common to them all are monopodial, rosette-formed assimilatory-shoots and lateral floral-shoots. The *Potentillas*, *Sibbaldia* and *Alchimilla alpina* have primary roots of long duration, and they distinctly belong to the type "Radix vel rhizoma multiceps"; the other *Alchimillas* branch less freely, and their primary root undoubtedly dies rather early. They live through the winter with their shoot-apices protected by the sheaths of dead and living leaves. To evergreens proper only *Pot. maculata* can be referred. It is however probable that other species also may live through the winter with a few green leaves, and as regards this point local differences no doubt take place. In species such as these which have no true winter-buds it is difficult to draw a sharp limit between the winter-green and the not winter-green habit, since the leaves of the following summer may grow out slightly in the preceding autumn. This uncertainty is no doubt the reason of the often contradictory records. — The leaf-structure would most nearly be characterized as mezomorphic in *Pot. emarginata* and *Alch. vulgaris* and as more or less xeromorphic in the others.

2. Wandering perennial herbs are *Pot. anserina* and the *Rubus*-species.

Pot. anserina has a rosette-formed, monopodial main shoot and lateral floral axes which behave as runners. Vegetative propagation takes place by the

individualization of the rosette-formed lateral shoots of the runners. Food-storing roots often occur. It lives through the winter without green leaves and with its shoot-apex covered by scale-leaves. It is typical for the leaf-structure to be slightly xeromorphic.

As features common to all the *Rubus*-species may be mentioned that they do not form rosette-shoots, that the floral shoots are terminal; and that they live through the winter without green leaves[1] and with their winter-buds covered by scale-leaves. *Rubus arcticus* wanders by means of its roots, and *Rub. saxatilis* by the development of certain shoots into aerial runners the apex of which is developed into a winter-bud situated at the surface of the ground. *Rub. chamæmorus* has scale-leaf-bearing underground runners. The leaf-structure in the two first-named is mesomorphic and in the last-named slightly xeromorphic.

There are at least two points connected with the shoot-structure of several of these *Rosaceæ* which appear to be favourable to plants living in Arctic climates, as regards the way the latter influence the plants, e. g. by desiccation (physiological desiccation) and by the shortness of the growth-period. A great many of the species, and more particularly those that are true Arctic (see p. 121), are more or less highly cæspitose, and may have in addition very closely packed shoot-masses (closest in *Pot. Vahliana*); it appears certain that by this method of growth the amount of transpiration is lessened, in that the outer shoots of the tuft protect the inner from the wind, and the shoot-apices are surrounded and protected by the dead masses of leaves.

[1] See p. 93.

From KJELLMAN's classical work "Ur polarväxternas lif" it has long been well known that the Arctic summer begins very suddenly and that a great many Arctic plants live through the winter with leaves which need only elongate slightly in order to attain full power of assimilation. The majority of the true Arctic species mentioned here live through the winter in this way; some even have small, green, half-opened leaves (*Dryas*). They have moreover no closed winter-bud surrounded by scale-leaves (except, e. g. *Rubus chamæmorus*) and with but very little room for the new foliage-leaves; but the "buds" are open, and the new organs — leaves and flowers — have ample room and grow out quickly, as soon as ever external conditions permit their doing so, and begin work in the short summer[1].

B. In the following species the flowers are formed during the

[1] As regards light-conditions in Arctic regions I would remark, that from Porsild's "Actinometrical observations from Greenland" (Arbejder fra den danske arktiske Station paa Disco, No. 4, Medd. om Grönland, XLVII, Köbenhavn, 1911) it is seen (from Tables II and III) that the mean light-total for the months May—August is about the same on Disco as in Denmark (Anholt). On comparing the assimilation-conditions of the plants on Disco and Anholt it is seen that the Greenlandic plants must, besides a lower temperature, also suffice with less light for their summer work than the Danish, the latter having longer time at their disposal. So far as I know it is an open question what use the plants make — if any — of the light of the midnight sun. The investigations made by Curtel (Rev. générale de botanique, Tome II, 1890) and Porsild (Meddel. om Grönland, XXV, 1902, pp. 25 and 26) regarding this point gave contradictory results. Besides Porsild, Wiesner has also studied the light-conditions in Arctic regions (Norway and Spitzbergen) and he finds by comparison with the Alpine regions of Central Europe that these are characterized not only by a greater light-intensity, but also by a greater amount of light in the period of vegetation. (Beitr. z. Kenntniss des photochem. Klimas im arct. Gebiet. Denkschr. math. nat. Cl. d. K. K. Ak. Wien. LXVII, 1908, and Beitr. z. Kenntniss des Lichtklimas von Tromsø, etc. Tromsø Museums Aarshefter, 24. Tromsø, 1901).

summer previous to the year in which they expand, viz. *Alchimilla alpina*, *Alch. vulgaris*, *Dryas octopetala*, *Potentilla emarginata* and *Rubus saxatilis*, all of which flower in June. It is probable that the great majority of the species behave as these, with the exception however of *Pot. palustris* in which the young flower-buds have not been observed until the spring of the year in which they expanded.

C. The absorbent roots often present anatomical peculiarities, for instance, a thin epidermis which is usually more or less collapsed is found in the majority of the Potentillas (*anserina*, *emarginata*, *maculata*, *nivea* and *pulchella*), and in addition in *Sibbaldia* and *Rubus saxatilis*. In *Rubus chamæmorus* it is destroyed early. A stronger epidermis occurs in *Pot. palustris*, where it is very small-celled, and in the *Alchimilla*-species where there is a tendency to throw it off entirely, because the thin-walled exodermis ruptures. In *Pot. emarginata*, *P. nivea* and *P. pulchella* the radial and the outer walls of the exodermis are very highly thickened, and this cell-layer is also very strong in *Rubus chamæmorus*. In the *Alchimilla*-species the cortical layer within the thin exodermis is fairly strong. In *Dryas*, *Rubus arcticus* and *R. saxatilis* the radial walls — and in the two last species also the outer walls — of the cortical layer outside the endodermis are very strong.

Ectotrophic mycorrhiza occurs in *Dryas;* and endotrophic mycorrhiza has been found in *Pot. anserina*, *Pot. emarginata*, *Pot. nivea*, *Pot. palustris*, *Pot. pulchella*, *Sibbaldia*, *Alchimilla alpina*, *Alch. acutidens* and *Rubus arcticus*. All the *Rosaceæ* mentioned here have probably mycorrhiza, except *Rub. chamæmorus*.

D. A continuous cambium is found in the perennial portion of the shoots in all the species. According to the nature of the tissue produced by the cambium the species may

be divided into two main groups. One, more herbaceous, in which the secondary formations consist of groups of vessels rich in parenchyma and separated by broad medullary rays; the Potentillas with the exception of *Pot. palustris* and *Pot. tridentata* belong to this group. Another, more lignified, in which the cambium produces a ring-shaped woody portion; to this belong the rest of the species. In *Dryas*, *Potentilla palustris.*, *P. tridentata*, *Sibbaldia* and *Rubus* are found medullary rays, one to a few cells broad; medullary rays are absent from *Alchimilla* except above the leaf-trace bundles ("Blattspurstränge"). In *Alch. alpina* and especially in *Alch. vulgaris* and *Alch. færoensis* the secondary wood-formations constitute only a comparatively small portion of the shoots, and these are then more herbaceous.

Bast occurs regularly only in *Dryas.*

In *Dryas*, from which, as already mentioned, an endodermis is absent, cork is formed in the inner part of the cortex; in all the others which have an endodermis, a periderm is probably always formed in the outermost layer of the pericycle (cf. SOLEREDER[1]). *Dryas*, only, has a scaly bark ("Schuppenborke") formed of centripetally developed phellogens which develop only cork-cells without intercellular spaces. In the other species, on the other hand, the periderm consists of one layer of cork-cells alternating with usually three layers of phelloid-cells. It contains large intercellular spaces, which are however absent from the inner side of the cork-layers in the great majority of the species.

SOLEREDER (l. c.) who also describes the periderm has found intercellular spaces in the phelloid in *Pot. palustris* and *Poterium sanguisorba;* in his opinion this suggests a resemblance to aërenchyma and he regards it as an adap-

[1] Anatomie d. Dicotyled. Stuttgart, 1899, p. 348.

tation to life in bogs in these species. It is true that respiration in the inner part of the shoots is facilitated by the presence of the intercellular spaces in the periderm, but the comparison with aërenchyma does not appear appropriate when we consider that species from extremely dry habitats, such as *Pot. tridentata*, *Pot. nivea*, *Alch. alpina* and others have a quite similar structure of the periderm. A contribution to the explanation of the structure of the periderm in these *Rosaceae* may perhaps be found in the fact that it no longer functions only as a protection from excessive transpiration, as for instance in *Dryas*, but that it has also developed into a very important starch-storing organ; at any rate, a periderm with this function requires an ample supply of oxygen so that the necessary condensations and hydrolyses can take place in it. — It may be mentioned that a similar periderm also occurs in the roots of the species which have been investigated, with the exception of *Dryas* and *Rubus arcticus*. As regards this point the reader is referred to Martha Bunding[1] who has investigated the root-cork in many *Rosaceae* and finds as a rule intercellular spaces in the herbaceous species, but not in the woody or shrubby (cited from Freidenfelt).

E. Special food-storing organs are absent except in *Pot. anserina* which frequently has spindle or club-shaped food-storing roots of a peculiar anatomical structure. Otherwise reserve food-material is found in the root (many of the species have primary roots of long duration and considerable size) and in the perennial portions of the shoots. The tissues which contain reserve food-material are the

[1] Structure of the Cork Tissues in Roots of some Rosaceous genera. Publ. of the Univer. of Pennsylv. New Ser. No. 5. Contrib. fr. the Bot. Laborat., Vol. 2, 1898. (Unfortunately, the paper has not been available to me).

phelloid, the pericycle, the medullary rays and the wood-parenchyma; and in the pith, especially the peripheral part.

The reserve food-material consisted especially of starch in all the species which have been investigated in regard to this point; but in several of these species (*Dryas*, *Alchimilla*, *Pot. emarginata*, *Pot. nivea*, *Pot. palustris*, *Sibbaldia*, *Rubus saxatilis*) it has been demonstrated that during winter the starch disappears more or less completely and is replaced by fat.[1] Probably during autumn the starch is converted into fat, and then during spring the fat is again converted into starch. Similar conditions are well-known as regards several trees. It is apparently a common occurrence among perennial herbs and dwarf-shrubs that during winter the starch is replaced by fat, the amount of fat increasing from October or November and reaching its maximum in January or February, then during spring it disappears entirely in temperate regions; this is at least the case as regards a great many Danish species. On the other hand, there are a number of species in which no fat is visible during winter; as an example, the food-storing roots in *Pot. anserina* may be mentioned. While, as mentioned above, fat is absent from the depository organs of the herbs during summer in Denmark, I have, in *P. nivea*, *P. emarginata* and especially in *P. pulchella* (from N. E. Greenland) found fat in rhizomes and roots throughout the whole summer; this is probably due to the comparatively low temperature during summer in Arctic regions.

F. A great many of the species have leaves which in one way or other illustrate xeromorphy. Transpiration is lessened (a) by a hairy covering: in several of the species the under side of the leaf is densely matted or hairy, espe-

[1] Indicated by use of Sudan III.

cially in *Dryas*, *Pot. nivea*, *Alch. alpina* and others; (b) by a revolute leaf-edge, which is found especially in several *Dryas*-forms and in *Pot. pulchella* f. *humilis;* (c) by sunken stomata, which are found in *Alchimilla*, *Pot. palustris*, *Pot. tridentata*, and *Sibbaldia*, while in several of the species, which have a dense hairy covering upon the under side of the leaf, the stomata there project slightly above the leaf-surface. For the rest, stomata occur on both surfaces of the leaf in almost equal number in *Sibbaldia* only; of the other species, stomata are entirely wanting upon the upper side in the following: *Alch. alpina*, *Alch. færoensis*, *Dryas*, *Pot. Vahliana*, *Rubus* and *Sorbus*. Lastly, transpiration must also be lessened by (d) a thick outer wall in the epidermis, and here *Dryas* and especially *Pot. tridentata* may be mentioned; and (e) by the mucilaginous covering of the inner wall in the upper epidermis (pectin-mucilage). This is found in *Dryas*, *Pot. maculata*, *Pot. nivea*, *Pot. palustris*, *Pot. pulchella* and *Pot. tridentata*, *Sibbaldia* and *Sorbus*. Very often not all the cells are mucilaginous; in *Pot. tridentata* besides the inner wall the outer wall is also somewhat mucilaginous and in *Pot. maculata* a few mucus-cells were also found in the lower epidermis. The importance which should at any rate be attached to a cellulose-mucilaginous covering of the inner walls of a leaf-epidermis is among others mentioned by Volkens[1], who is of the opinion that such mucilage in the cells does not function as a water-reservoir, but checks transpiration in the same manner as does a gelatinous layer which is spread over a slightly evaporating surface of water (compare also Warming, 1887).

The mesophyll in the leaves of the species which have been investigated has a very ordinary structure, and it shows only to a slight degree such adaptations to

[1] Die Flora der Aegypt.-Arab. Wüste. Berlin, 1887, pp. 43—45.

external conditions as are evident in the structure and hairy covering of the epidermis of at least several species. The palisade-tissue in almost all the species consists of 2—3 layers of cells; in the *Alchimilla*-species only, there is usually a single layer of very long palisade-cells. In these the relation between length and breadth is as 4 or 5 to 1; the same relation is also found in the upper layer of palisade-cells in *Sorbus;* but in the remaining species the palisade-cells are only 2—3 times as long as they are broad; they are often somewhat barrel-shaped. In all the species the relation between the thickness of the leaves and the thickness of the palisade-tissue is about $\frac{2}{1}$; as regards this point some variations have been found to occur in various species, but such special records of the nature of the habitats as are necessary in order to be able to understand such variations have unfortunately not been at my disposal. In the majority of the species there are large intercellular spaces in the palisade-tissue. In *Pot. tridentata* these are however small, and as regards the mesophyll, this species has the most xeromorphic leaf, while the least xeromorphic is that found in *Rubus saxatilis* and *R. arcticus.*

The transpiration-parenchyma is throughout of loose structure and consists of short, branched cells. Large slit-like lacunæ occur commonly within the subepidermal layer on the lower surface of the leaf (e. g. in *Dryas, Pot. pulchella, Alch. alpina*).

The species may be divided into two groups according to the anatomy of the leaves; viz. into those species which have a mesomorphic leaf-structure and those which have more or less well-marked xeromorphic leaves. To the first group belong *Rubus saxatilis* and *Rub. arcticus, Alch. vulgaris* and *Alch. færoensis*, and perhaps also *Pot. emarginata* and *Sorbus americana.* The remaining species

are referable to the other group; particularly, *Dryas*, *Pot. tridentata*, *Pot. nivea* and *Pot. pulchella* (especially f. *humilis*). Some understanding of the leaf-structure in the different species may be gained by a consideration of the habitats. Species of the first group, with the exception of *Pot. emarginata*, are generally associated with relatively favourable soil, moreover, none of them — again with the exception of *Pot. emarginata* — are true Arctic species. The majority of the species in the other group are natives of dry localities such as fell-fields, rocks and heaths, and a great many of them are High Northern species, while two of them are bog-plants. The few species which may be regarded as more or less evergreen belong to this group. It does not appear, however, that the leaf-structure is governed thereby to any special degree, perhaps, however, with the exception of *Pot. tridentata*; it is tempting, more particularly on account of the leaf-structure in this species, to conclude that it is an evergreen; but beyond the surmise that a few of the summer leaves may undoubtedly live through the winter I am prepared to state nothing. In *Dryas* the outer wall in the upper epidermis of the leaf is somewhat thicker in the leaves which live through the winter than in the summer leaves which die away during autumn; but the common xeromorphy in the leaf-structure of this species must upon the whole be due to other reasons, because the number of the summer leaves is far greater than that of the leaves at the shoot-apex which live through the winter. One of the reasons for the xeromorphy in the *Dryas*-leaves is undoubtedly that already mentioned: the dryness of the soil, or, at any rate, the physiological dryness of the heaths and rocks where the plants grow. A similar consideration to that which holds good for *Dryas* may be applied to the other species which may occasionally be

found with green leaves during winter. *Pot. maculata* is however an exception, as it must undoubtedly be called a true evergreen; but in comparison with the other herbaceous *Potentillas* its leaf-structure does not exhibit any special xeromorphic characters.

Among the 14 species of Arctic *Ranunculaceæ*, which I have investigated[1], there are only two, at most three species, the leaves of which have a xeromorphic character, viz. *Thalictrum alpinum* and *Coptis trifolia* which have leathery leaves, which in the latter live at least two years, and *Ran. glacialis* with a somewhat succulent leaf which has a well-developed palisade-tissue. Of the remaining species all the land-plants have a decidedly mesomorphic leaf-structure. By comparison of the individual leaf-tissues in the species of *Ranunculaceæ* and *Rosaceæ* which have been investigated the difference between the two families is distinctly seen.

The epidermis in all the *Ranunculaceæ*, with the exception of certain forms of *Ran. acer.*, is glabrous or only slightly hairy. The outer wall of the epidermis of the upper leaf-surface, except in *Thalictrum alpinum* and *Coptis trifolia*, is thin, not above 2μ thick, and the walls are not mucilaginous as in the *Rosaceæ*. In the paper cited it is recorded that chlorophyll was usually found in the epidermis of the leaf of the Arctic *Ranunculaceæ* which had been investigated, but I did not observe this in the *Rosaceæ* which I have had for investigation. The stomata in our *Ranunculaceæ* are always situated on a level with both leaf-surfaces, and as in the *Rosaceæ*, they occur especially upon the lower surface of the leaf; three of the species have, however, the majority of their stomata upon the upper

[1] The Structure and Biology of Arctic Flowering Plants, I. 6. *Ranunculaceae* by Knud Jessen. Medd. om Grönland, XXXVI, Kobenhavn, 1911.

surface of the leaf, viz. *Ran. glacialis*, *R. hyperboreus* and *R. reptans*. The palisade-tissue is on an average somewhat more strongly developed in the *Rosaceæ* than in the *Ranunculaceæ*, and the intercellular spaces are usually smaller. It is recorded that the palisade-tissue in the *Ranunculaceæ* constitutes about one-half of the thickness of the mesophyll, but in several of the species it is, however, considerably less thick, e. g. *Anemone Richardsoni*, *Ran. Pallasii*, *Ran. pygmæus* and *Ran. nivalis*. The respiratory tissue is on an average looser in structure in the *Ranunculaceæ*. Several of the *Ranunculi* have leaves which in their anatomical structure recall the type which is common among woodland plants in temperate regions, thus especially *R. pygmæus* and *R. nivalis*, and a similar structure is found in *Rubus arcticus* and *Rub. saxatilis*.

The fact that the leaves of the *Ranunculaceæ* which have been investigated, are, as already mentioned, on the whole, to a greater extent mesomorphic than are those of the Arctic *Rosaceæ* is I find, partially explained — as in the *Rosaceæ* — by a consideration of the habitats. It is commonly stated that the Arctic *Ranunculaceæ* prefer damp localities, often bogs; thus *Ranunculus reptans*, *Ran. hyperboreus*, *Ran. lapponicus*, *Ran. Pallasii* and also *Ran. affinis*, *Ran. nivalis*, *Ran. pygmæus*, *Ran. sulphureus* and *Ran. glacialis* are mountain plants that live near the snow line in soil saturated with melting snow. *Anemone Richardsoni* lives by preference in copses, and *Thalictrum alpinum* and *Coptis trifolia* are met with in similar localities, or at any rate on luxuriant heaths. *Ran. acer*, on the other hand, often occurs on rather dry and stony soil, and in such localities its leaves are more hairy. We have, however, a peculiar instance of the fact that different plants react differently under apparently the same conditions. Thus, both *Potentilla palu-*

stris and *Rubus chamæmorus* show characters in their leaf-structure which undoubtedly should be regarded as agents serving to prevent excessive transpiration, and yet they grow in *sphagnum*-bogs as do *Ran. Pallasii* and *Ran. laponicus*, the leaves of which I should characterize more closely as mesomorphic-hydrophilous — a fact which indicates that the adaptation of plants is not evidenced solely by morphological conditions.

G. In the majority of the species the flowers are fairly conspicuous, least so in the *Alchimilla*-species and in *Sibbaldia*, but here they are gathered into more or less considerable inflorescences; *Sorbus* has richly flowering corymbs, but in the remaining species the flowers are either solitary or gathered into usually few-flowered cymes. Two species have red flowers, viz. *Pot. palustris*, and *Rub. arcticus;* the following have white flowers: *Pot. tridentata*, *Dryas*, *Rub. chamæmorus*, *Rub. saxatilis* and *Sorbus*; the rest have yellow petals. All the species undoubtedly produce honey, which is secreted by the inner side of the hypanthium; in several species a disk is developed (*Pot. tridentata*, *Sibbaldia* and *Alchimilla*). A slight perfume has been noted in a few species only. Well-marked hercogamy occurs in only a few of the species; *Rubus chamæmorus* is dioecious, *Dryas* is andro-monoecious and *Pot. palustris* is highly protandrous. The others are homogamous or have, at the most, a short preliminary unisexual stage. Slight protandry has thus been observed in *Pot. tridentata*, *Pot. maculata*, *Dryas* (some of the hermaphrodite flowers) and *Rubus arcticus*, while *Pot. anserina*, *Pot. emarginata*(?), *Dryas* (some of the hermaphrodite flowers) and *Sorbus* are slightly proterogynous. It must be assumed that self-pollination can take place in all species except in the *Alchimillas*, *Rub. chamæmorus* and *Pot. palustris.* There are only very sparing notes to hand as regards direct

observations of insect-visitors, in true Arctic regions, to the species in question, viz. only in the case of *Pot. emarginata*, *Pot. nivea*, *Pot.emarginata* and *Dryas*, which were visited by flies and other diptera.

H. Many of the Arctic *Rosaceæ* mentioned here have a very considerable area of distribution. Eight of the species are circumpolar or almost circumpolar — of these *P. pulchella* and *emarginata* are distributed only in the Arctic zone; the others extend far southwards, and of these the two bog-plants *P. palustris* and *Rubus chamæmorus* are especially confined to the low lands, while the others (*P. nivea*, *maculata*, *Sibbaldia* and *Dryas octopetala*) are confined to mountainous districts in temperate regions. *Pot. tridentata* and *Pot. Vahliana* are also true Arctic species, but their area of distribution is smaller; this is also the case with *Dryas integrifolia*, which in America, however, has advanced somewhat southwards. *Pot. anserina* is almost cosmopolitan. According to Wolf the Tertiary circumpolar land was probably the home of the original *Potentillas*, whence they have migrated southwards. He ascribes to those groups, among others to which our *Potentillas* belongs, a very high age, and regards several as palaeotypic; the majority of the species must be regarded as very old. *Dryas octopetala* and *Sibbaldia procumbens* are probably also originally true Arctic forms, which have afterwards extended towards the south. The great Glacial period may have helped them, together with *P. nivea* and *maculata*, to cross the Central European low land; they are also very old species.

Of these species only the following appear to have qualifications for wide fruit-dispersal: *P. palustris* and *P. anserina* by the agency of the water, *Dryas* by the wind and *Rubus chamæmorus* endozoically.

Another group of the species in question comprises

temperate forms, viz. *Rubus saxatilis*, *R. arcticus* and *Alchimilla vulgaris*; they have extended more or less further towards the north, and have in several places passed beyond the Polar Circle. To these *Sorbus americana* may also be referred. This and the two *Rubus*-species have endozoic or at least synzoic fruit-dispersal, and the *Rubus*-species (especially *R. arcticus*) have attained a very wide distribution.

Alchimilla alpina is presumably an Alpine form, which has probably during the Glacial period migrated northwards and has in Scandinavia passed over the Polar boundary (BUSER in SCHRØTER; l. c.).

12.—3.—1914.

9.

Cornaceæ.

By

Carsten Olsen.

1914.

Preface.

The material used for the following investigation is the property of the Botanical Museum in Copenhagen. A large material of *Cornus suecica*, preserved in spirit and collected at several places in Greenland has been placed at my disposal, also a smaller quantity of similar material from Finmark, other places in Norway, from Sweden and Denmark. Besides this, I have used dried material of *Cornus suecica* from Greenland, Iceland, the Færöes, Denmark, Norway, Sweden, Finland and North America.

Amongst the dried specimens from Greenland I found three specimens of *Cornus canadensis*, determined as *Cornus suecica*; these specimens were collected by A. Jessen, July the 28th 1894, on a small, remotely situated island, Inuarudgligak, near the southern point of Greenland (60° 23″). *Cornus canadensis* has not hitherto been known to exist in Greenland; certainly W. Meehan mentions it as found here, but Th. Holm, who has gone through his material from Greenland, has shown, that Meehan was probably not in position to determine his plants correctly, especially as he has not even collected the plant, but simply made a note of its occurrence. I have also had ample material of *Cornus canadensis* from North America and Japan.

Fig. 2 is drawn by Professor Warming; the photograph fig. 10 is taken by H. E. Petersen, mag. sc., while the remaining figures are drawn by myself.

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Cornus suecica L.

Norman, 1901, p. 322. Warming, 1887, p. 18, 34, 40, 75, 138. Rosenvinge, 1896, p. 67, 128, 161, 197, 198. Hartz, 1894, p. 57. Buchenau, 1859, p. 87. Sylvén, 1906, p. 135. Silén, 1905, p. 87. Willis & Burkill, 1903, p. 343. Sernander, 1901, p. 141, 142, 164. Sertorius, 1893, p. 622. Knuth, 1898, vol. 2, part 1, p. 51).

Cornus suecica is mostly found in the subarctic regions, and most frequently in the northern part of the Scandinavian peninsula, but is fairly common everywhere in Finland, Sweden, Norway and in the northern parts of Denmark. Elsewhere in Europe it is found near Reval, in Holstein and Pomerania, and the Alps, also in the Færöes and Iceland. Outside Europe it grows in West Greenland, in Labrador, New Foundland, Alaska and Baffinsland.

In Greenland it appears most frequently in "Urtelierne" and in thickets; Hartz says it is nearly always found in birch thickets and Rosenvinge, that it is also present in the willow thickets and on the heaths in the southern part. Its northern boundary in Greenland is according to *Rosenvinge*, at 69°14.

According to *Norman* it occurs in Finmarken in the birch woods, where it often by itself forms the undergrowth, growing closely like corn in a field.

The development of the shoots of *Cornus suecica* has been described by Buchenau (1859), and my own observations quite agree with his description. The rhizome is horizontal and bears opposite triangular scale-leaves, two to three centimeters apart. It is of several years duration, while the scale-leaves die already the first year; and from their base adventitious roots appear, with a rich ramification. In the axis of the scale-leaves buds develop, some becoming runners, resembling in all particulars the mother-

shoot, others remain dormant. The runners, which attain a length of up to 30 centimeters, finally turn their apex upwards, forming a stem with foliage-leaves, terminating with an inflorescence or else remaining vegetative. The perpen-

Fig. 1. *Cornus suecica.*
A, Flowering Plant; *B*, Apex of Runner (Godthaab, Greenland); *A*. about 3/4, *B*, 2/1.

dicular part of the shoot commences with a series of pairs of scale-leaves, red while fresh, but withering quickly; their number varies from 3 to 9 pairs, and is as a rule 5. The foliage leaves develop next, Danish specimens showing 4 to 8 pairs, those from the arctic 3 to 4 only.

Buchenau states, that the two uppermost pairs are closely placed, resembling a whorl; all the specimens from one Danish locality (Maglemose in Grib Skov) examined by me showed the same, while plants from other Danish localities did not. On arctic material I never found it.

The aërial part of the shoot attains a height of from 6 to 30 centimeters and is annual. The stem is quadrangular and has two opposite grooves (fig. 12), which change sides at each internode, the leaf pairs being placed at their lower ends. The scale-leaves, with which the perpendicular part of the shoot commences, support buds, the first pair excepted; and some of the buds develop next year into shoots with foliage leaves, growing upwards immediately, and showing no inclination to become runners. These shoots also commence with a number of red scale-leaves, after which follow foliage-leaves. The same ramification takes place the following year from the scale-leaf buds of these shoots, and so on, thus forming a tufty growth.

According to Buchenau, it is always the buds appearing in the axis of the second pair of scale-leaves which develop, so that all the shoots are placed at the same level. This is however far from always being the case, often it is from the uppermost pair of scale-leaves or the one next to this, from which next year's shoot develops, and often only one bud from a pair of scale-leaves develops, although the second one can very well develop later during one of the following years.

The buds which are to develop into shoots next year, are in the autumn of a considerable size and the first two pairs of leaves are brown and formed like bud-scales. The whole shoot completely formed is inclosed in the winter-bud, also the inflorescence and the first indications of the buds to develop the 2nd year.

The leaves of *Cornus suecica* fall in the autumn, while

the stem is yet fresh; towards the winter it dies, but can very well remain standing in a withered state for several years. The winter buds are located near the surface of the ground, and the plant is thus, as regards its life habit, a hemikryptophyte. Buds are formed in the axis of the foliage leaves, which however are very small, and as a rule only the buds of the uppermost pair of foliage leaves develop; at the time of flowering they are only small, but during the summer they develop into large side branches. I have noticed a Danish specimen, not flowering, where all the buds of the foliage leaves were developed, with the exception of the lowest pair.

The leaf is ovate and sessile, with two or three veins diverging from each side of the midrib, near its base. On arctic specimens the uppermost pair of leaves (100 specimens were measured), had an average length of 19 mm, the average width being 12 mm. On Danish specimens, however, the average length was 28 mm with an average width of 17 mm, 100 specimens also being measured in this case. The leaves of the Danish specimens thus distinguish themselves by being considerably larger than those from the Arctic.

The seedlings have been described by SYLVÉN; the cotyledons are shortstalked, ovate-lanceolate, about 7 mm long. The primary root is strongly ramificated, and the development of the adventitious roots seems only to take place during the second period of growth; only few internodes are formed on the aerial shoot during the first year. The hibernation takes place by means of buds in the axis of the cotyledons, which next year develop into new aërial shoots, and the formation of runners only commences several years later.

In Greenland the flowering takes place in July and August. The inflorescence is a head-like or umbelliforme

cyme, surrounded by four yellowish-white involucrals, by which, as is well known, the whole inflorescence gets the appearance of one single big flower, with four petals. Each flower has a short stalk, about 2 mm long; the sepals are very small, and the petals, of which one is often elongated, have a dark red-violet colour, and are turned sideways. The style is surrounded at its base by an annular brown disc; the stamens are turned to the side in the spaces between the petals.

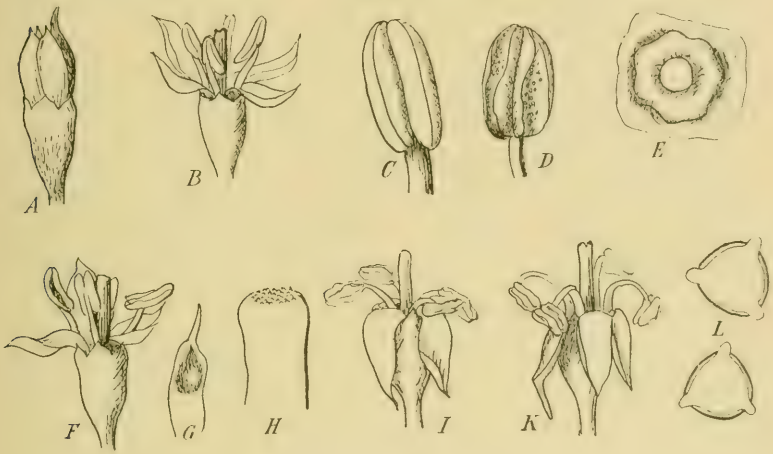


Fig. 2. *Cornus suecica.*

A—*E* from West Greenland, (Sukkertoppen, 16th August); *A*, Flower in bud ($^{10}/_{1}$), *B*, Flower in full bloom (just opened); *C*, Anther, not open ($^{25}/_{1}$); *D*, Anther, open ($^{25}/_{1}$); *E*, Discus, seen from above ($^{25}/_{1}$); *F*—*K* from Northern Norway (Tromsø, 24th July) ($^{10}/_{1}$); *F*, Flower with one anther (to the left) open ($^{10}/_{1}$); *G*, The elongated petal (see fig. *A*); *H*, Part of style with stigma; *J*, Empty anthers, pollen apparently on stigma; *K*, Same, but filaments more curved; *L*, Two pollen grains, from Northern Norway (Bosekop) ($^{410}/_{1}$); (*A*—*K*, Eug. Warming del.).

Concerning specimens from "Sukkertoppen" Warming writes in his notes from Greenland: "Slight protandry is noticed. Simultaneous with the opening of the petals, the stamens extend and the anthers open, but the stigma is not yet fit to retain the pollen; when this shortly afterwards happens, the anthers are still full of pollen and self-pollination possible, though I think, not easily, by reason of the spread of the filaments (Fig. 2 *B*, *F*); as the flowers

stand so very close to each other, it is more likely they could reach the nearest ones and deposit pollen on their stigmas, and, as a matter of fact, I have seen the anthers of neighbouring flowers in close proximity to a flowers stigma".

WARMING found the same form of development in arctic Norway (Tromsø, Alten) and pure homogamy was only found once. The pollination takes place by insects, which are guided to the flowers by the four big and petal-like involucrals; according to WILLIS and BURKILL the visitors are few, mainly of the order of *Diptera*.

The pollen grains, which are only few in number, have three strongly projecting pores (fig. 2).

Deformity of the inflorenscence is not quite uncommon; sometimes the involucral is partly and even completely green. WARMING mentions such deformities in his notes from "Sukkertoppen"; in the same locality he found specimens with 6 or 7 involucral leaves.

The fruit is a drupe; the stone is two-celled, one of which nearly always remains barren; the ripe fruits, red in colour, are found in Greenland in August and September. The dispersal takes place by animals (HESSELMAN found 40 stones in the excrements of a *Larus marinus*), and partly by means of water; the plant often grows near watercourses, and the stones being lighter than water, will often be carried far away; SERNANDER found them thrown up by the sea near a small island in the Baltic, more than 400 km from its nearest habitat.

Anatomy.

The leaf is dorsiventral, with a pallissade tissue of one layer of cells and a pronounced spongy tissue (fig. 4). The epidermis of the upper surface consists of very large cells, while those of the epidermis of the lower surface are

smaller and with undulating sidewalls. This undulation is more pronounced in leaves of Danish specimens than in those from the Arctic (fig. 3). The sidewalls of the upper surface are also undulating, but in a lesser degree, and also in this case is found the same discrepancy between Danish

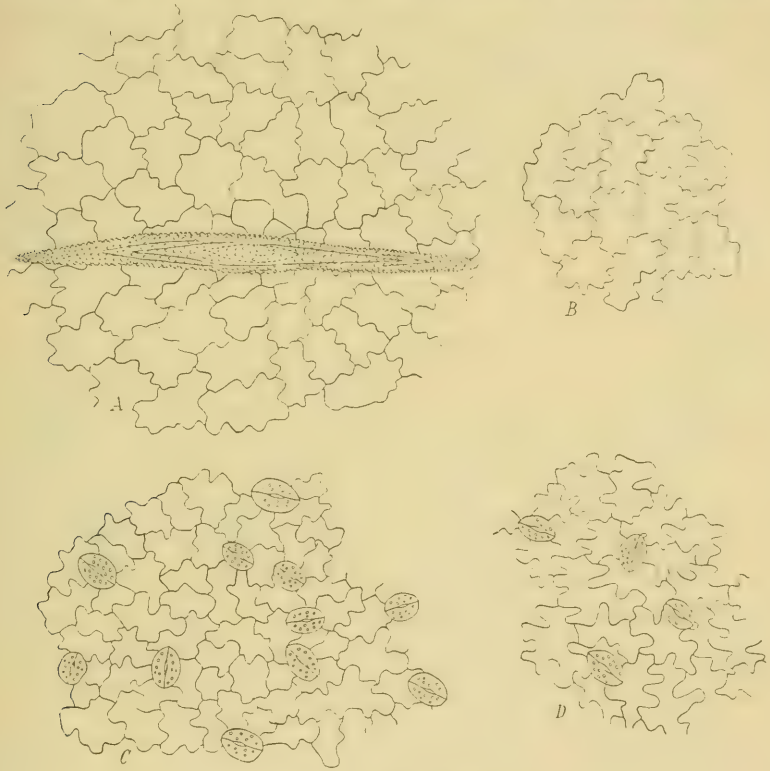


Fig. 3. *Cornus suecica.*

A, Epidermis, upper surface, with a two-armed hair (Sukkertoppen, Greenland); *B*, Epidermis, upper surface (Maglemose, Denmark); *C*, Epidermis, lower surface (Sukkertoppen, Greenland); *D*, Epidermis, lower surface (Maglemose, Denmark); *A*, *B*. *C* and *D* about $^{130}/_{1}$.

and Arctic leaves, though less pronounced. The cuticula is thin on both sides, and shows opposite the larger veins fine stripes, running parallel to the longitudinal axis of the leaf.

Only the lower surface has stomata, these are placed

over the level of the other epidermal cells, more pronounced on Arctic than Danish leaves. As to the number of stomata on a given area, they are perhaps more numerous in the Arctic specimens than in Danish. The table below gives the number of stomata pr. Sq. m. m. of a number of Danish and arctic leaves:

Danish Leaves		Arctic Leaves	
Locality	Number of Stomata pr. □ mm	Locality	Number of Stomata pr. □ mm
Maglemose(Grib Skov)	70	Egedesminde	100
Vildmosen	100	Tromsø	84
Hæsede	78	Nunatsuk	82
Silkeborg	85	Julianehaab	120
Skibsted	66	Ilua	134
Vildmosen	127	Godthaab	75
Mariager	82	Sukkertoppen	109
Hillerød	70	Sukkertoppen	79

Among other differences between leaves from the Arctic and those from temperate localities, the following is particularly pronounced and has shown itself to be very constant: The Arctic leaf is thicker than the Danish (fig. 4). This substantial difference is chiefly due to the strongly developed spongy tissue of the Arctic leaf, while the length of the cells of the palisade tissue is rather smaller than in Danish leaves. Besides this, the Danish leaves have a more loosely built mesophyll with the palisade cells only loosely connected, diverging below, and the spongy tissue has large intercellulars and more slender cells than is the case with arctic leaves (fig. 4, *C—D*). The relation between the size of the spongy tissue and that of the palisade tissue of Arctic and Danish leaves is plainly given by the following measurements of leaves from eight different Danish localities and a similar number from the Arctic.

Danish Leaves				Arctic Leaves			
Locality	Thickness of			Locality	Thickness of		
	Leaf	Palisade tissue	Spongy tissue		Leaf	Palisade tissue	Spongy tissue
Maglemose (GribSkov)	174 μ	66 μ	90 μ	Godthaab ...	231 μ	51 μ	138 μ
Hæsede....	174 -	57 -	78 -	Sukkertoppen	234 -	54 -	135 -
Mariager ..	168 -	57 -	81 -	Egedesminde.	210 -	57 -	120 -
Helsingør..	174 -	66 -	75 -	Julianehaab .	246 -	60 -	150 -
Hillerød ...	177 -	66 -	78 -	Nunatsuk ...	246 -	72 -	144 -
Skibsted...	174 -	66 -	81 -	Ilua.....	210 -	54 -	120 -
Vildmosen .	180 -	75 -	78 -	Tromsø.....	189 -	48 -	114 -
Silkeborg ..	156 -	60 -	66 -	Sukkertoppen	240 -	60 -	138 -

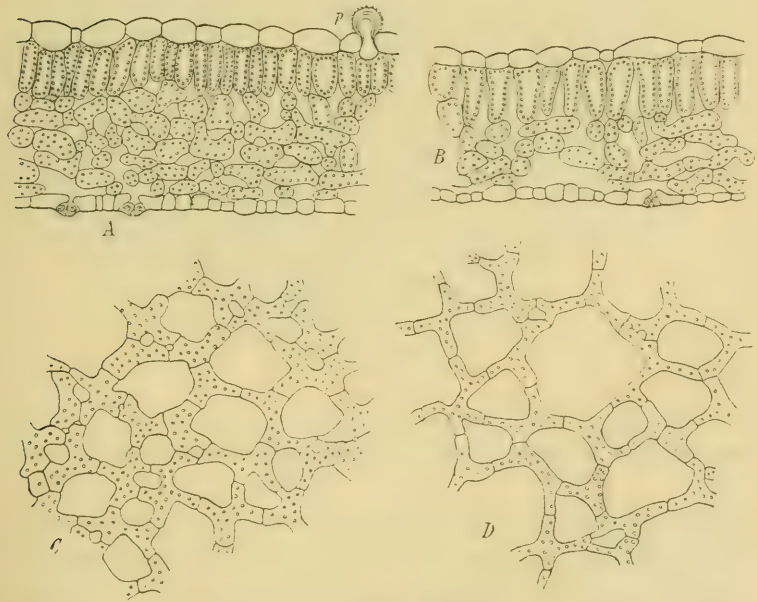


Fig. 4. *Cornus suecica.*

A, Transverse section of leaf, p, two-armed hair (Godthaab. Greenland); *B*, Transverse section of leaf (Maglemose, Denmark); *C*, Section through the spongy tissue, parallel to the surface (Godthaab, Greenland); *D*, Section through the spongy tissue (Maglemose, Denmark); *A*, *B*, *C* and *D* about $^{136}/_{1}$.

The upper as well as the under surface of the leaf is provided with large two-armed hairs (Malpighia-hairs), fig. 3 A, shaped like a pickaxe, the upper-surface having, on the same area, about three times as many as the under surface; they are one-celled and the stalk is exceedingly short (fig. 4 A). The

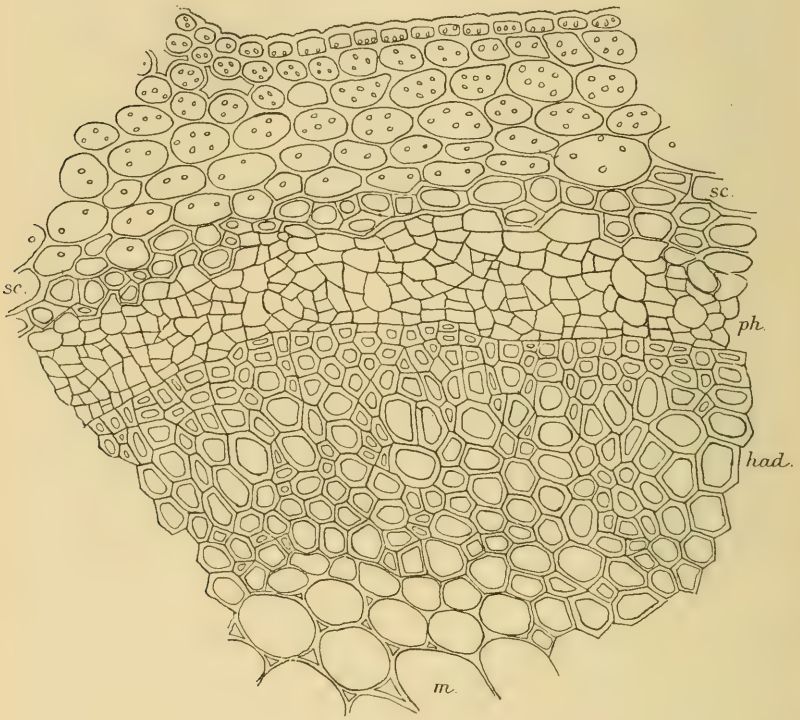


Fig. 5. *Cornus suecica.*
Transverse section of stem; *ph*, Leptom; *had*, Hadrome (Egedesminde, Greenland); about $^{270}/_{1}$.

surface of the hair (the short stalk excepted) has numerous projections, thickenings of the walls, and the latter plainly show several layers which are much thickened; the lumen is extraordinarily small and seldom reaches the ends of the arms, which are consequently solid (fig. 3, 4).

The main veins of the leaves have on their under

surface, below the phloëm, a slight sclerenchyma, which is not present in the smaller ones.

The Stem (fig. 5). The aerial shoot is annual. The epidermis has thickened outerwalls and is covered by a thin cuticula, striped parallel to the stem's longitudinal axis;

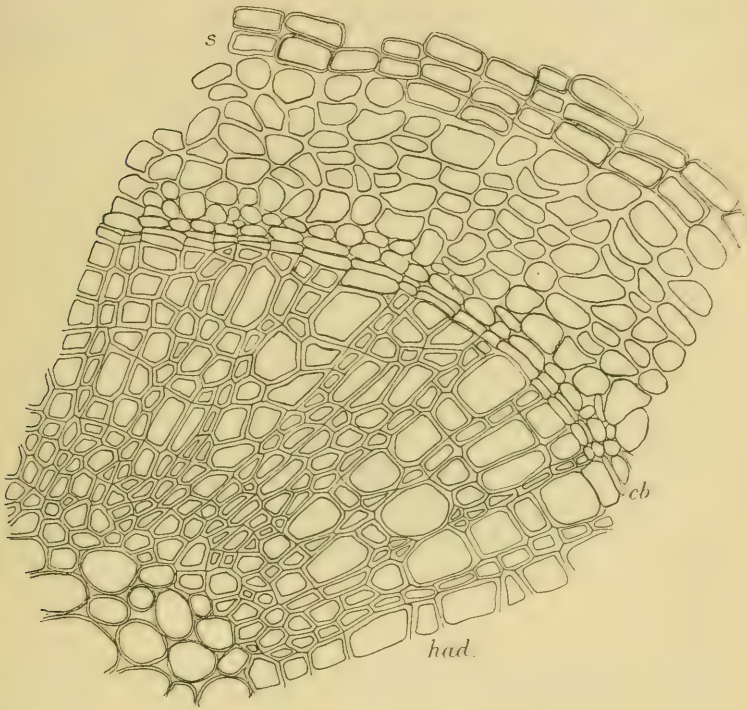


Fig. 6. *Cornus suecica.*

Transverse section of rhizome; *S*, Cork; *cb*, Cambium; *had*, Hadrome (Egedesminde, Greenland), about $^{270}/_{1}$.

stomata are present. Five layers of large chlorophyllaceous bark-cells follow inside the epidermis, and after these a more or less developed annular schlerenchyma, consisting of elongated parenchymatic cells, with much thickened walls (fig. 5, *sc*). The phloëm appears inside this annular sclerenchyma and, like the woody tissue, forms a coherent ring

round the stem. The cambium is rudimental in the fully developed stem, its activity soon ceasing as the whole of the woody tissue is already formed while the stem is quite young.

The wood consists chiefly of spiral and pitted vessels, tracheids and wood-parenchyma. The vessels are fairly narrow, and in transverse sections, angular; the pitted vessels have ringpores, while the wood-parenchyma has single

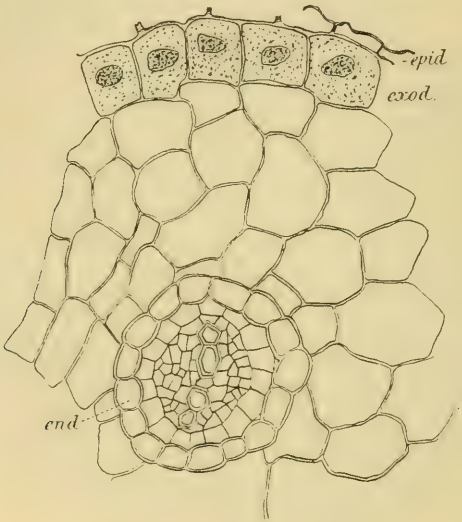


Fig. 7. *Cornus suecica*.

Transverse section, showing primary structure of root; the epidermis is dead and partly fallen off; *exod*, Exodermis; *end*, Endodermis (Sukkertoppen, Greenland) about $^{330}/_{1}$.

pores; medullary rays are not present, but starch is found in the wood-parenchyma, and inside the latter a medulla with large cells runs in the longitudinal direction of the stem.

The rhizome (fig. 6) is covered with cork, consisting of rather thickwalled cells and formed sub-epidermally. The bark-cells are arranged rather irregularly inside the cork, they are somewhat thickened collenchymatically and contain starch, which as far as *Cornus suecica* is concerned, always

consists of composite granules. On the innerside an even transition from the bark-cells to the phloëm is to be found. As in the stem, the wood consists of a coherent ring, and has rather indistinct annual rings. The secondary wood consists of trabecular and ringpored vessels, together with tracheids and wood-parenchyma, this latter being rich

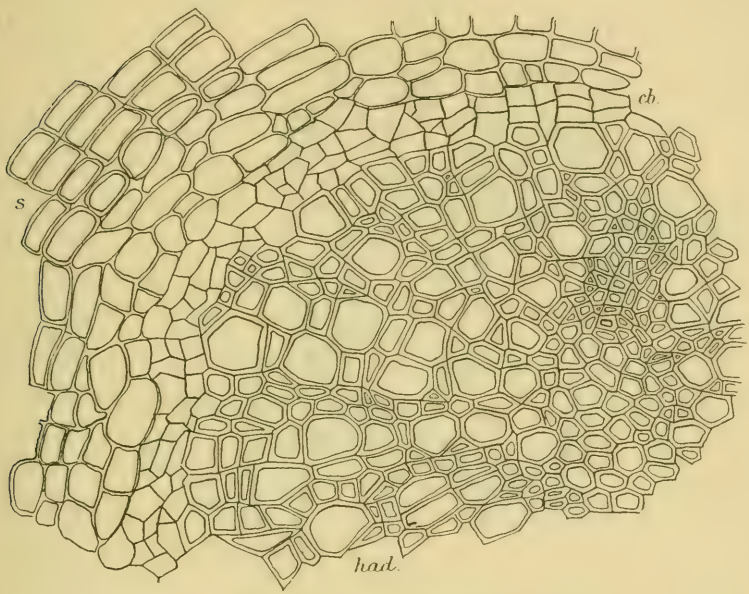


Fig. 8. *Cornus suecica.*

Transverse section, showing secondary structure of root; *S*, cork (Greenland); about $^{312}/_{1}$.

in starch. Medullary rays are not present, the medulla consisting of large cells filled with starch.

The bark-cells of the rhizome contain large quantities of tannin, which is also found in the bark-cells of the stem and in the leaf.

The Root: the primary structure is diarch, it has a suberized rather thickwalled endodermis and a distinct pericycle (Fig. 7).

The bark consists of rather large cells; the epidermis dies away very quickly, and remains as a loose sheath round the very young root, while the exodermis, the cells being yet well filled with protoplasm, soon produces a layer of corky tissue with thickened cells, and resembles otherwise the cork of the rhizome.

The secondary root (fig. 8) is on the whole of the same

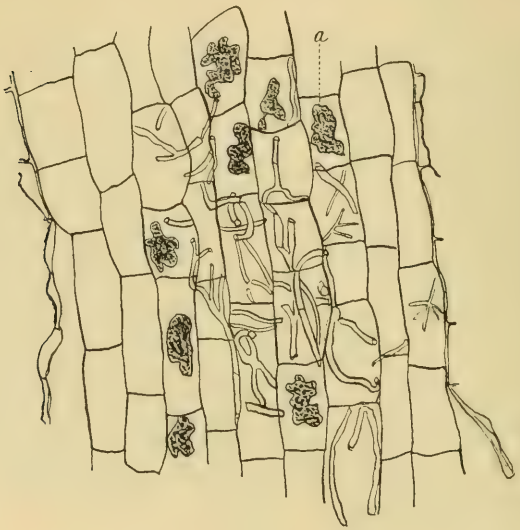


Fig. 9. *Cornus suecica.*

Tangential, longitudinal section through the bark of a young root, containing mycorrhizae; *a*, destroyed hyphae (Greenland) about $^{240}/_{1}$.

structure as the rhizome, the exception being that no medulla is found.

Endotrophic mycorrhiza is always found in the young root, in Arctic as well as in Danish specimens (fig. 9); the fungal hyphae are rather thick and not very closely knotted together, as is most often the case with roots having endotrophic hyphae. The hyphae are both inter- and intracellular, and in the cells are also found irregular or coral-shaped clumps, probably destroyed hyphae, which like the former

colour strongly when treated with Hansen's haematoxylin. The cells containing these lumps or living hyphae contain no starch, other cells are rich in this.

Cornus canadensis L.

Sertorius, 1893, p. 619; Lovell, 1898, p. 386; Holm, 1895, p. 544; Meehan, Th., 1892, p. 376; Meehan, W., 1893, p. 211.

Cornus canadensis (fig. 10) is found most frequently in North America; it is met with throughout Canada, with the exception of the most northern parts, from New Foundland and Labrador to Southern Alaska. Its southern boundary passes through the states of West Virginia, Ohio, Indiana, Wisconsin, Minnesota, Nebraska, Colorado and California. It is found also in the northern Islands of Japan, and now, as mentioned in the preface, in the most southerly part of Greenland, in the small, remotely situated island, Inuarudgligak. It does not reach as far North as *Cornus suecica*, which e. g. is met with at Baffinsland, where *C. canadensis* is not found, whereas it is found considerably further South. In North America *C. canadensis* has its habitat in damp, cold woods (*Pinus*, *Larix*) and in thickets, and evidently grows in more shady places than *C. suecica*; in Japan it grows in the mountains.

Fig. 10. *Cornus canadensis* from Inuarudgligak in Greenland, about $^3/_4$ (H. E. P. phot.).

As to the structure of the shoot, this corresponds in the main to that of *C. suecica*; all the foliage leaves are

placed in a whorl at the top of the stem, though occasionally one or two leaf pairs are found lower down. The leaf-whorl is formed by the suppression of the uppermost internodes on the main as well as on the secondary axis. In contrast to *C. suecica* the leaves are said to be everlasting (ASCHERSON and GRAEBNER); they are considerably larger and tapering at the base; and also differ as regards the venation; in *C. suecica* the veins all diverge from the base of the leaf, while in *C. canadensis* the two uppermost side-veins diverge from the midrib somewhat higher up.

The involucral leaves are as a rule larger than those of *C. suecica.* The petals are green, one of them often having an awl-shaped elongated point. In material from North America I have found specimens with red petals edged with green, which together with other characteristics made them form a transition in appearance to *C. suecica*[1]). The three specimens from Inuarudgligak which constitute the whole material from Greenland had green petals.

The biology of the flower has been treated by LOWELL, who writes: "As the flower-bud approaches maturity the filaments grow rapidly, breaking apart the petals at the base, and protruding as four V-shaped arches. If at this stage the awl-shaped appendage is touched by the body of an insect, or by a needle, the petals are instantly reflexed, the elastic filaments straighten, and a minute shower of pollen is projected upward. In fully matured flowers a faint snap may be heard. Self-fertilization is prevented by the immaturity of the stigma. Both stamens and petals soon fall away, and the capitate stigma, composed of white

[1] I have seen a similar intermediate specimen from Neriak on the East coast of Greenland (61° 3″); the involucral leaves were very large, and the petals red, edged with green; it had 2 pairs of large, opposite leaves of which the uppermost pair supported short-jointed shoots; the leaves tapered at the base and the venation and anatomy were quite similar to those of *C. canadensis.*

papillae, subsequently matures. Though self-fertilization is prevented by proterandry there may occasionally be observed, resting against the stigma, the anthers of neighbouring flowers. The honey is secreted in a very thin layer by a dark brown ring at the base of the style[1].

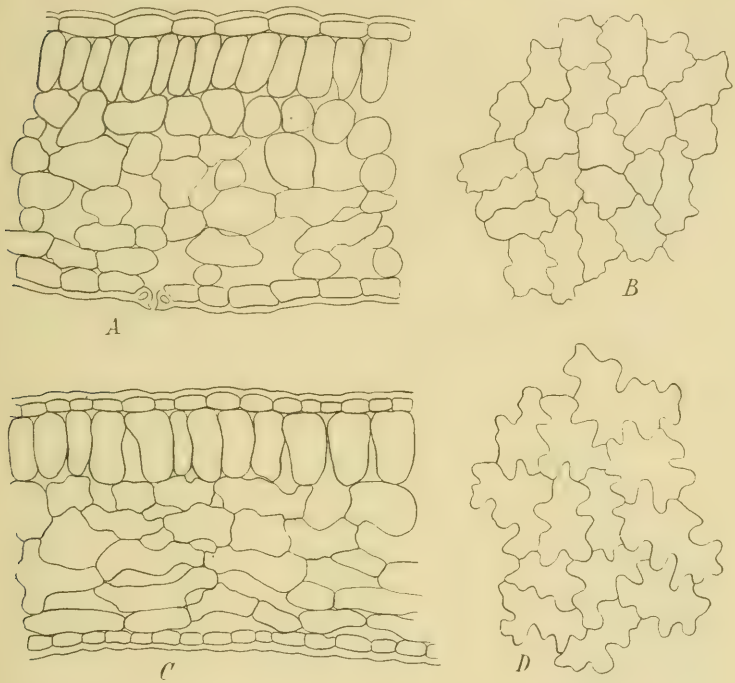


Fig. 11. *Cornus canadensis.*

A, Transverse section of leaf (Inuarudgligak, Greenland), *B*, Epidermis, upper surface (Greenland); *C*, Transverse section of leaf (Minnesota); *D*, Epidermis, upper surface (Minnesota); *A*, *B*, *C* and *D*, about $^{185}/_{1}$.

[1] Thomas Meehan reports having observed, that *C. canadensis* is partly monoecious, partly dioecious. He has only seen plants with ripe fruit, not any flowering specimens, and found, that the inflorescences of some plants were quite sterile, others had a single berry in the middle of the cyme, while others again were rich in fruits; from this he draws his conclusion. All the individuals I have examined have been hermaphrodite, and as Lowell, who has studied the biology of the flower, does not

Anatomy.

The Leaf. The leaf is dorsiventral as in *C. suecica*, but differs in having the epidermal cells of about the same size on both surfaces; also by the cells having strongly thickened outer walls, this latter being caused by the cellulose-membrane; the cuticula is quite thin. The palisade-cells are rather thick and short. Apparently there is the same difference between leaf specimens from Greenland and those from more southerly latitudes, as is the case with those of *C. suecica*. The leaves from Greenland are thicker than those from further South, and the extensiveness of the spongy-tissue is much greater in comparison to the palisade-tissue.

The following table gives a few measurements of leaves from different latitudes:

Locality	Thickness of leaf	Extensiveness of Palisade-tissue	Extensiveness of Spongy-tissue
Greenland	90 μ	16 μ	56 μ
Vancouver Island	60 -	18 -	30 -
Minnesota	55 -	20 -	26 -
New Foundland	70 -	16 -	37 -
Turnavik (Labrador)	50 -	19 -	25 -
Specimen from the Botanical Garden at Berlin	77 -	27 -	40 -

On the American specimens the epidermis of both surfaces have strongly undulating sidewalls, while this is much less pronounced in those from Greenland (Fig. 11). Stomata are only present on the under surface; the specimens of *C. canadensis*

mention diclinous flowers, these must consequently be very rare, if existing at all.

from Greenland having 160 of these pr. square mm, while specimens from Canada had only c. 140 pr. sq. mm.

The Stem. The stem is very much like that of *C. suecica*, the transverse section being however somewhat different. As Fig. 12 shows, the stem of *C. suecica* seen in transverse section is more barrel-shaped, and the groove not very deep, while that of *C. canadensis* is considerably deeper, making the stem "four-winged"; besides this, the circumference of the medulla of *C. canadensis* is quadrangular, while that of *C. suecica* is round. In *C. canadensis* the distal part of the wings of the stem consists of collenchyma while such is practically missing at this place in *C. suecica* (Fig. 13).

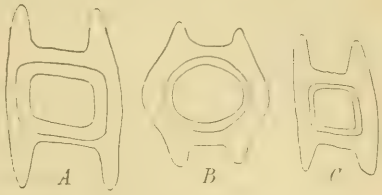


Fig. 12.

Transverse sections of stems. *A*, *Cornus canadensis* from Vancouver Island; *B*, *Cornus suecica* (Greenland); *C*, *Cornus canadensis* from Greenland; *A*, *B* and *C* about $^{12}/_{1}$.

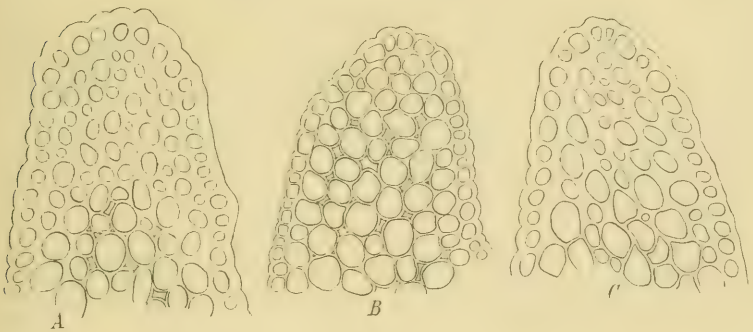


Fig. 13.

Transverse section of the winged part of the stem. *A*, *Cornus canadensis* from Vancouver Island; *B*, *Cornus suecica* from Greenland; *C*, *Cornus canadensis* (Greenland); *A*, *B* and *C* about $^{175}/_{1}$.

The sclerenchyma in the bark of *C. canadensis* is often greatly developed in vigorous specimens, while it is about

missing in poorly developed plants, e. g. in the specimens from Greenland.

The anatomic structure of the rhizome and the root is exactly like that of *C. suecica.* Tannin is present throughout the plant.

The mycorrhizas of *C. canadensis* and *C. suecica* are alike.

Summary.

Cornus suecica is a distinct mesomorphic plant which completely lacks xeromorphic characters; such are however found in *C. canadensis*: the epidermal cells of the leaves of this species have thickened outer walls, which is correlated to the fact of the leaves being perennial. The more loose construction of the mesophyll of Arctic plants mentioned by BØRGESEN[1] does not apply to the species here dealt with; on the contrary, the Arctic specimens of *C. suecica* have a mesophyll of a much closer structure than the specimens from more southerly localities. Besides this, the leaves of *C. suecica*, grown in Arctic localities, are distinguished by being smaller, but decidedly thicker than those of specimens from Denmark. The spongy-tissue is very strongly developed in Arctic specimens.

[1] Bidrag til Kundskaben om arktiske Planters Bladbygning (Botanisk Tidsskrift, Bd. 19, 1895; also in "Journal de Botanique", vol. 9, Paris 1895).

10.

Caprifoliaceae.

Linnaea borealis L.

By

O. Hagerup.

1915.

The present investigation is carried out with the aid of material from the herbaria belonging to the Botanical Museum at the University of Copenhagen; it is brought from many different localities by several investigators. Besides this, material from Denmark, preserved in spirit has also been used. All material from Greenland was dried, which has caused difficulties, especially as regards the leaf anatomy; some material was also collected by WARMING in Northern Scandinavia. *Linnaea* being a plant about which many investigations have been made and many papers written, especially GIGER'S monograph, a more complete treatment is superfluous, and in this general statement it has only been necessary to mention the main points.

As regards the distribution of the plant the above named paper may be referred to.

As to the localities in Greenland in which *Linnaea* is found, the following are represented in the herbaria:

1. Præstefjeldet near Holsteinsborg, in a thicket of *Salix glauca*, *Empetrum* and *Vaccinium uliginosum*, collected by WARMING and TH. HOLM.
2. Ivnarsuak in Tasermiut Fjord, leg. F. BENJ. PETERSEN.
3. Ivigtut, leg. AUG. BERLIN.
4. Kvannit Sarok in Diskofjord (Lat. 69° 33′ N.), copiously flowering in the outskirts of willow thickets; leg. MORTEN P. PORSILD; this being the most northern locality in which *Linnaea* has been found in Greenland.

The following literature has been used (complete list of literature available is given in Gigers monograph).

Brenner, M., 1909: Några Linnaea-former i Finland (Medd. af Soc. pro fauna et flora Fennica, h. 34, p. 89—97 og h. 35, pag. 56).
Giger, Emil, 1913: Linnaea borealis L., eine monographische Studie (Beihefte zum Bot. Centralblatt, Band XXX, Zweite Abt.).
Gundersen, 1910: Recherches anatomique sur les Caprifoliacées (Thesè; Paris).
Leist, K., 1889: Über den Einfluss des alpinen Standortes auf die Ausbildung der Laubblätter. (Mittheil. d. Naturf. Gesellsch. v. Bern.)
Norman, J. M. 1895: Norges arktiske Flora, II, pag. 324. Kristiania.
Petersen, O. G., 1901: Diagnostisk Vedanatomi, pag. 93. København.
Poppius, B. R., 1903: Blombiologiska iakttagelser (Acta Soc. pro fauna et flora Fenn. 25, No. 1).
Schröter, C., 1904: Das Pflanzenleben d. Alpen, I. p. 235.
Sernander, R., 1891: Studier öfver skottbyggnaden hos Linnaea borealis L. (Bot. Notiser 1891, p. 225).
Silén, F., 1905: Blombiologiska iakttagelser i Kittilä Lappmark (Medd. af Soc. pro fauna et flora Fenn., h. 31, p. 88).
Sylvén, N., 1906: Om de svenska Dikotyledonernas första förstärkningsstadium; 1 (Kungl. Svenska Vetenskapsakademiens Handlingar, Band 40, No. 2, p. 65).
Wagner, A., 1892: Zur Kenntniss des Blattbaues d. Alpenpflanzen und dessen biol. Bedeutung. (Sitz. Ber. der Wien. Akad., math.-nat. Cl., p. 615, Bd. C 1, Abt. 1).
Wittrock, V. B., 1879: Om Linnaea borealis (Bot. Not. 1878, p. 17, 49, 83, 122 and 1879, p. 9, 137).
— 1907: Linnaea borealis (Acta Horti Bergiani, Bd. 4, No. 7).
Wydler, H., 1859: Morphologische Mittheilungen (Flora N. R. 17, p. 1).

Germination. According to the literature *Linnaea* seldom produces germinable seeds in Central Europe, while seeds from the North germinate within a few weeks. Wittrock has found a seedling grown under natural conditions. The further development of the seedling has been examined through cultures by Giger; the results are briefly as follows: the germinable power of the seeds lasts for at least three years, and the development of the seedling proceeds slowly, especially at first; during the second year the main axis, consisting of 2—4 internodes, inclines horizontally towards the ground, and becomes

the rejuvenating runner, bearing buds, which, as described later, become fructification or assimilation shoots, respectively. In its third year the plant has reached its full development, consisting of a main root (which can live a few years), some adventitious roots, and two succesive long-shoots.

Morphology of the Stem. *Linnaea borealis* L. is an evergreen woody plant (not an undershrub) with a long, creeping main axis, sending off rootlets, and bearing two kinds of erect, short shoots, which according to their function may be called, respectively: assimilation and fructification shoots (Wittrock).

The Rejuvenating Shoot. The rejuvenescence takes place by the terminal bud of the main axis yearly producing a creeping shoot, 6—45 centimeters long, consisting of 10—16 internodes, the individual length of which is lessened towards both ends of the shoot. Wittrock mentions, that these shoots can reach an age of up to 13 years. The plant can quickly spread over large areas. The terminal bud is covered by rudimentary green leaves, which do not wither during the next period of growth, but on the contrary lengthen somewhat in their outer half, and act as organs of assimilation. As a rule all the leaves of these rejuvenating shoots support buds, which during the next period of growth develop into one of the three kinds of shoots. Generally however one of the two buds of a leaf-pair becomes a "dormant bud", while the other, distinguished by its greater size, develops into an

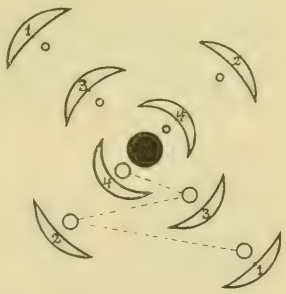


Fig. 1.
Diagram, showing the more vigorous buds (the larger circles) supported by the leaves placed on the underside of the rejuvenating shoot.

assimilation or fructification shoot. Through the twisting and turning of the petioles, the leaves apparently stand in two rows, whereas in reality they are placed crosswise opposite. It is always the leaves nearest the ground, which support the most vigorous bud, and as a consequence of this, the short-shoots are placed in a zig-zag line with an ascending base. Fig. 1 illustrates this, which disagrees with the general view, that the leaves have been placed in two rows by the twisting of the stem.

New rejuvenating shoots may appear by the development of older and younger buds from all three kinds of shoots, which enables the plant to spread in all directions (see Giger).

The Assimilation Shoot develops, as already mentioned, from a side bud on the horizontal rejuvenating shoot. It is characterised by a short axis (4—6 cm high) with 4 or 6 internodes, and especially by a relatively great number of foliage leaves, which gain for it the name of assimilation shoot; besides these leaves, one or two pairs of scale leaves are present, which quickly wither. The axillary buds seldom develop; the rejuvenescence is, as in the rejuvenating shoot, monopodial; the terminal bud, covered by 1 or 2 pairs of scale leaves, develops during the following period of growth into a shoot similar to that of the previous year; this is continued for 3 or 4 years, when at last the shoot ceases its function. New assimilation shoots may also develop from older or younger side shoots or end shoots, of any of the other kinds of shoots (see Giger).

The Fructification Shoot consists of two different parts, viz. a lower vegetative part, which is perennial, and an upper floral one, which is annual.

Of these the lower one is much like the just mentioned assimilation shoot, but differs by nearly always sending out adventitious roots from its ascending base. The shoot ter-

minates in a floral part, which withers every year, and the rejuvenescence takes place by a vigorous bud, situated in the axis of one of the upper leaves, so that the fructification shoot, contrary to the two other forms of shoots, becomes a sympodium.

The floral part consists of a long thin internode, the terminal bud of which does not reach development under natural conditions. Below this point is a pair of bracts, each supporting a flower, the inflorescence thus being a two-flowered cyme. Just below each flower, three alternating pairs of bracts are found; the uppermost pair grows bigger as the fruit ripens, finally quite enclosing it. The whole of the floral part of the shoot is covered by glandular hairs, which have a many-celled head, and a long, two- or three-celled stalk. These hairs increase in numbers towards the upper end of the shoot; they are especially numerous on the uppermost pair of bracts, which (according to Giger) produces additional glandular hairs towards the time of maturity; by means of their sticky secretion they are said to further the dispersal of the fruits by causing it to become attached to passing animals.

The Flower. A zygomorphy is often present both in calyx and corolla; it varies however much, as does also the colour of the corolla; both of these peculiarities have been closely studied by Wittrock (1907), to whose work reference is made. The flowers have a pleasant, strong scent of vanilla, and on the innerside of the corolla, at the base of the lowermost petal, is a nectarium partly covered by long hairs. The secreted fluid shows distinct sugar reaction.

The anthers are didynamous and develop simultaneously with the stigma (according to Warming). The list of the visiting insects (Giger) shows a comparatively great number of *Diptera*, honeyseekers with short proboscis, which

without any difficulty can enter the corolla by reason of its large opening. Besides, visits by *Lepidoptera* and *Hymenoptera* have been observed. The ovary is trilocular, two compartments containing several ovules which do not develop, while the third contains one only, which however is fit for development.

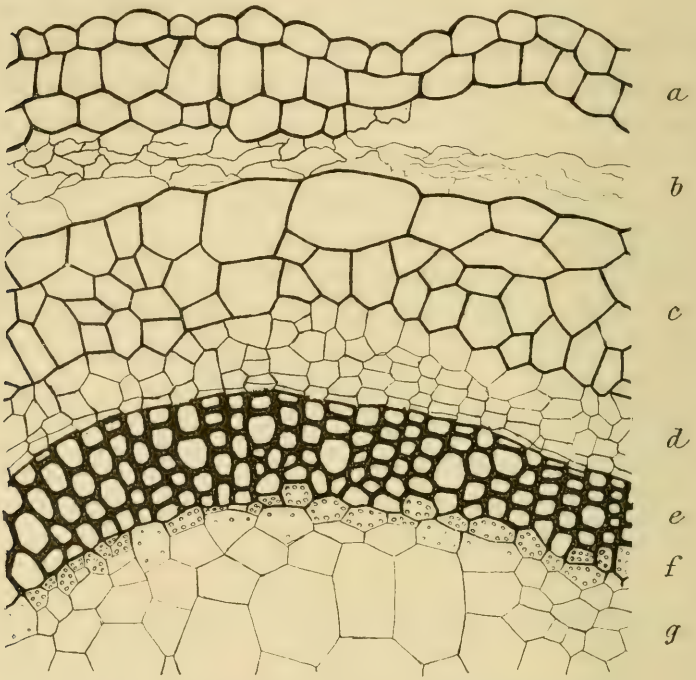


Fig. 2. Transverse section of the rejuvenating shoot (material from Greenland).

Compared with material from Denmark, the Arctic *Linnaea* has a compact growth, owing to shorter internodes; this mode of growth causes the deviating habitus, peculiar to many Arctic plants.

Anatomy of the Stem. The bark and the wood together only amount to half the diameter of the stem, the pith being relatively strongly developed. The bark passes through

peculiar phases of development. The epidermis and hypodermis (Fig. 2 *a*) start to fall off in the 3rd year, through the destruction of the underlying 2—3 layers of cells (Fig. 2 *b*); the protective function of the former is then taken up by the 1—(5) layers of large bark cells (Fig. 2 *c*) underneath, the walls of which become woody. During the 4th year however, this protecting layer is also partly thrown off, owing to the cells immediately underneath being similarly destroyed; the outer cells then form a third protective layer by a strongly developed formation of cork.

The diameter of the stem is about the same all over, as the growth in thickness keeps pace with the decrease in diameter, caused by the falling off of the several layers of bark. Under the bark is the cambium (Fig. 2 *d*) and under this the wood (Fig. 2 *e*), which yearly grows a little in thickness and shows annual rings. The wood consists of vascular tissues, tracheids, libriform-cells, wood-parenchyma and medullary rays.

The original transverse walls have the appearance, even in the fully developed vessels, of a grate, consisting of very thin, parallel staffs. The vessels lie scattered in the wood, but not in such great numbers as the tracheids; all kinds of transitions to these latter are however found, and the circular or oblong pores have the same trabeculate arrangement.

The greater part of the wood consists of tracheids; libriform-cells and wood-parenchyma are rarely met with, and are of quite subordinate importance. Between the pith (Fig. 2 *g*) and the wood are found a few layers of cells, which both in shape and position form the transition between the medullary cells and the tracheids; as the figure shows, their walls have circular pores (Fig. 2 *f*).

The numerous medullary rays consist of 4—8 radiant rows of cells placed vertically above each other; they are always well filled with starch, which can however also be the case with the cells of the living bark.

Short- and long-shoots have in the main the same anatomic structure.

The Leaf. Its duration is from 2 to 3 years; in shape it varies somewhat, most often it is ovate, but elliptical-round or nearly kidney-shaped leaves are also found. As a rule 2 faint incisions are to be seen on each side of the leaf, but some variations are also found in this respect; it is

Fig. 3. The leaf.

Epidermis: *g*, lower surface (material from Greenland); *d*, lower surface, *o*, upper surface, with palisade cells added (material from Denmark).

pinnately veined. Scattered hairs are present, of the same type as those on the stem; on the lower surface of the leaves are some glandular hairs, with a short one-celled stalk and a many-celled head, which secretes a sticky substance in which fungus spores are often caught and germinate.

The mesophyll shows that the leaf is a typical shade-leaf, in conformity with its usual habitat (Fig. 4).

The epidermis contains chorophyll; the cells are largest on the upper surface (Fig. 3).

The perpendicular walls are undulating with thickened outer ends (Fig. 4). This was especially pronounced on the

material from Greenland, where the walls also were thicker. The stomata, which are only found on the lower surface, are somewhat projecting, oval, and of the usual structure (Fig. 3).

The following table shows the average number of sto-

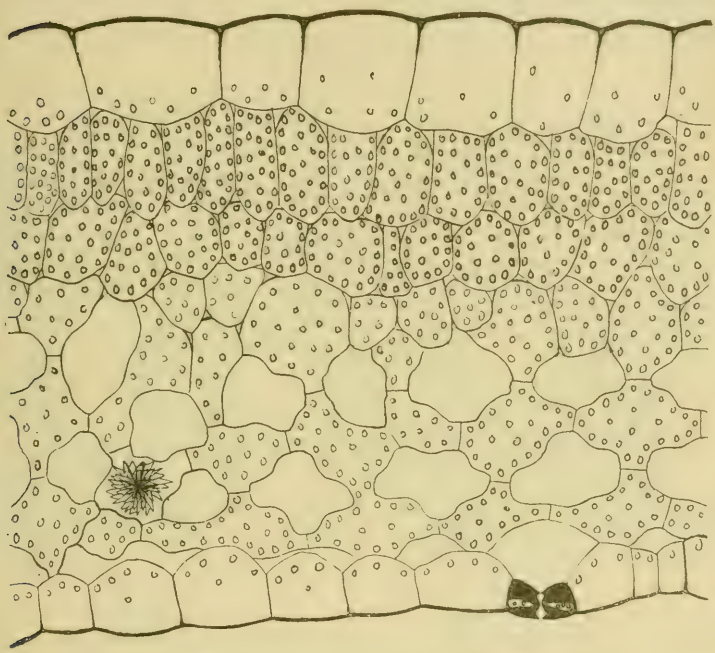


Fig. 4. Transverse section of leaf (from Denmark).

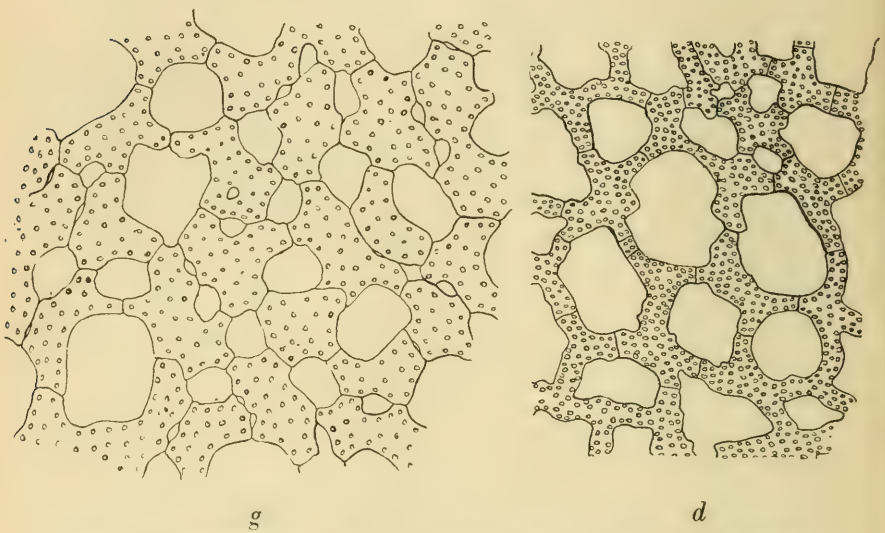
mata on $^1/_{10}$ mm^2 of 6 leaves from Denmark compared with 6 from Greenland:

Leaf	1	2	3	4	5	6	pr. mm^2
Danish . .	49	39	51	45	39	55	463
Arctic . . .	40	44	47	40	48	45	440

On 1 mm^2 the average was about 450 stomata.

The undulation of the perpendicular cell walls of the epidermis is still more pronounced on the lower surface of the leaf than on the upper surface. Besides, the material from Greenland also showed a thickening, and larger undu-

lations of the perpendicular epidermis walls, on the lower surface, than was the case with leaves from Denmark. The cell (see Fig. 3 *g*), which carries a glandular hair, has however straight cell walls, and the spongy tissue underneath is without intercellular spaces. The mesophyll has a pretty, regular structure rich in intercellular spaces, especially so in the spongy tissue, but also in the palisade tissue (Fig. 4).



g *d*

Fig. 5. The lowermost layer of spongy tissue, viewed from above; *g*, from Greenland; *d*, from Denmark.

The leaves from Denmark had, with scarcely any exception, one layer of short, broad palisade cells only, while those from Greenland had two; further, the spongy tissue of the Danish leaves had throughout a looser structure than those from the Arctic.

These relations are the opposite to what has been found by examination of other Arctic plants with regard to leaf-structure; the explanation is probably, that *Linnaea* in Greenland grows on open heaths, and consequently is not, as the Danish plant, a typical shade-plant.

The spongy tissue, generally consisting of three layers, is connected with the palisade cells by a layer of collecting cells.

The leaves from Greenland are, as is generally the case, of a smaller size than those from outside the Arctic zone.

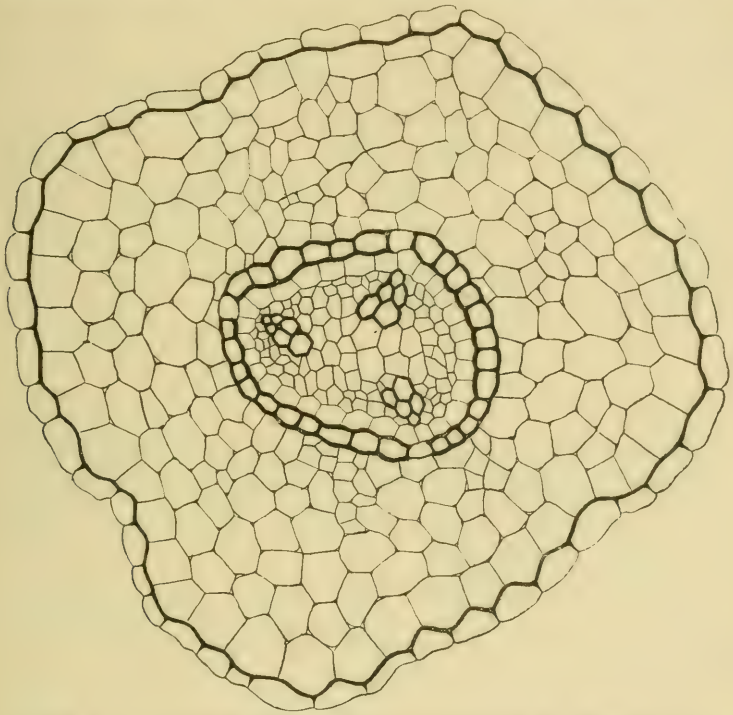


Fig. 6. Transverse section of triarch root (from Greenland).

The Root (Fig. 6). The primary root dies quickly and is replaced by the fairly numerous adventitious roots, which sprout from nodes on the rejuvenating and fructificating shoots, and ramify freely in the ground; this latter generally contains many decaying plant tissues, why mycorrhiza formations might be expected on the roots, but such have not yet been found. The epidermis of the root has thickened inner walls; the outer walls however are thin and, together with the root-hairs, decay during the second

year. The exodermis, with the remainder of the epidermis, thus becomes the outermost layer; its cell walls are slightly thickened. Underneath is the starch-carrying bark, which occasionally exceeds several times in thickness the diameter of the central cylinder. Towards the centre, the bark adjoins an endodermis, the cells of which has thickened walls, those of the passage cells excepted. During the fourth year the whole of the bark is forced off, and the pericambium becomes phellogen, which forms a cork, consisting of about 10 cell layers (Giger). The central cylinder is diarch to pentarch, and outermost is a distinctly bounded pericycle. Wood, to fill the central cylinder, is quickly formed; its anatomic structure is practically identical with that of the stem, and shows distinctly annual rings.

Summary.

When compared with material from Denmark, *Linnaea* from Greenland is distinguished by the following characteristics:

The stem has shorter internodes, giving the plant a more compact appearance.

The leaves are smaller with slighter incisions, and the perpendicular walls of the epidermis cells are thicker and have more pronounced undulations.

The mesophyll has smaller intercellular spaces and larger palisade tissues.

11.

Primulaceae.

By

Fr. J. Mathiesen.

1916.

For this work, entrusted to me, the necessary material has kindly been placed at my disposal by the Botanical Museum of the University in Copenhagen and by the Riksmuseum in Stockholm. I have throughout had the kind advice and guidance of Professor E. WARMING, and wish to tender my hearty thanks for his great kindness and courtesy. I am also greatly indebted to Dr. C. H. OSTENFELD, Inspector at the Botanical Museum, for the willing help extended to me on several occasions.

With the exception of figs. 6 A—I and 10, which were placed at my disposal by Prof. WARMING, all the others have been prepared by me. The anatomical sketches were drawn with the help of Abbe's drawing-apparatus and reduced to half-size when reproduced. The lens-combination used in drawing is given in the text for each figure, one index is the number of the Zeiss apochromatic, the other that of the compensation-eyepiece.

The following species have been examined: —

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Primula egaliksensis 169
— *sibirica* 176
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— *farinosa* var. *groenlandica* 187
— *nivalis* 190
Androsace septentrionalis 194
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Primula egaliksensis Wormskj.

Lit.: Flora Danica, t. 1511. Lange, 1880, p. 71; 1887, p. 260. Warming, 1886 a, p. 24. Widmer, 1891, p. 119. Rosenvinge, 1892, p. 684. Børgesen, 1895, pp. 223, 225, 236, 237. Pax and Knuth, 1905, p. 77.

Herbarium and alcohol material from South-West Greenland collected by J. Vahl (1828), Rosenvinge (1888), Meldorph (1900), and Deichmann (1906). Also, as alcohol material, seedlings from seeds collected in Greenland, and grown in the Botanical Garden at Copenhagen (one of these is illustrated in fig 1, a).

A perennial herb of the common Primula type (Warming 1884, pp. 33, 37 and 38; Pax in Englers bot. Jahrbücher, 1889). The vertical rhizome is very short, since the lower end dies away from year to year; it is richly covered with adventitious roots, the duration of which must also be about a year. New adventitious roots had already appeared on specimens (gathered in July) where the buds, which continue the growth of the rhizome, had as yet only developed one pair of foliage leaves. The young roots were comparatively thick at their base (1.5—2 mm), and the cortical cells were full of starch. On the other hand, the

roots of the preceding summer had already begun to decay and were completely emptied of starch.

The leaves are arranged in a $\frac{2}{5}$ spiral. They vary somewhat in form and size, but with no apparent regularity in the variations, either as to arrangement or stage of development. The principal bud is placed in the axil of the uppermost foliage leaf, and, as mentioned, it had already developed several foliage leaves by the middle of the summer; as the result of further increases during the summer, a rosette of 6—8 leaves is formed. The growth of the bud ceases temporarily during the autumn, some of the leaves remaining as scale-leaves, to form a protective covering for the younger growth, which next spring will develop into ordinary foliage-leaves. These scale-leaves may be found at the base of the spring-rosette as late as July, but only in a very damaged state. Unfortunately, I had at my disposal no buds gathered during the winter, but it is probable that the bud-scales contain starch, as is the case with kindred species.

Fig. 1. *Primula egaliksensis.* *a*, Seedling from the Botanical Garden, Copenhagen, ($^3/_1$) *b*, Young plant from Igaliko ($^{27}/_7$ 1888); *x*, the two first leaves of the autumnal rosette (about $^2/_1$).

The principal bud has sometimes been found to develop its peduncle during the same year as the parent shoot, and this even on plants showing relatively poor development, so that the plant may have two inflorescences flowering about the same time. Vegetative augmentation-shoots may be formed by small leaf-rosettes developed from some of the

microscopic buds, found in the axils of many of the foliage leaves (WIDMER, p. 10).

I have not been able to prove the presence of dimorphic flowers in this species (see E. WARMING 1886 a, p. 24). The length of the style varies only slightly, the majority of the flowers examined showing the stigma placed as in fig. 2, *a*. Self-pollination may occur, as the pollen and the stigma in the same flower seem to be fully developed at the same time. In *Flora Danica* the stigma is figured as extending a trifle above the anthers. The corolla is 5—8 mm. in diameter, the colour being white, with a yellowish ring in the throat. (Fig. 2.)

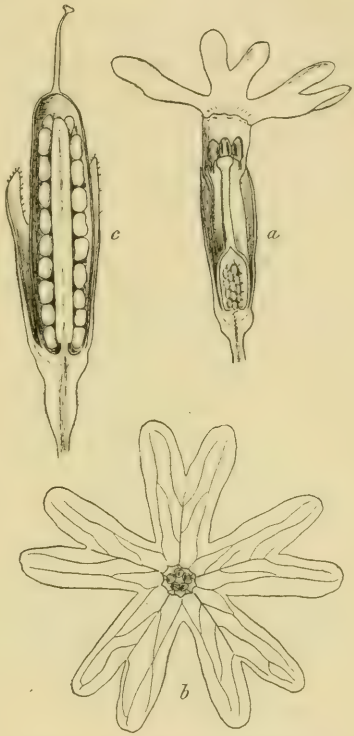

Fig. 2. *Primula egaliksensis*. *a*, Longitudinal section of a flower, the stigma is seen level with the base of the anthers, ($^5/_1$). *b*, The corolla-limb of a somewhat larger flower: in the throat the anthers are seen, ($^5/_1$). *c*, Longitudinal section of a ripe fruit, (about $^6/_1$). (Igaliko, $^{27}/_7$ 1888.)

The peduncle increases in length after flowering, as in the case of *Pr. stricta*.

Anatomy. A transverse section of the young primary root (fig. 3, *A*) shows the central cylinder to be very thin, only $\frac{1}{5}$ of the diameter of the root; the fourth layer of the cortex seems to be in process of formation. The primary root is diarch. Fig. 3, *B*, shows the central cylinder with the endodermis of a very young adventitious root. The cells of the cortex are filled with starch, except the outermost layer, which functions as an exodermis; this is

also the case in the primary root. As the root gets older, the vessels increase in number, the epidermis dies away, after which the cortical cells become emptied of starch and finally perish. Crystals of a calcium salt, single as well as aggregate, are found in the bark, especially in the exodermis of the older roots.

The Rhizome. A transverse section through the lower part of this shows the severed adventitious roots and the

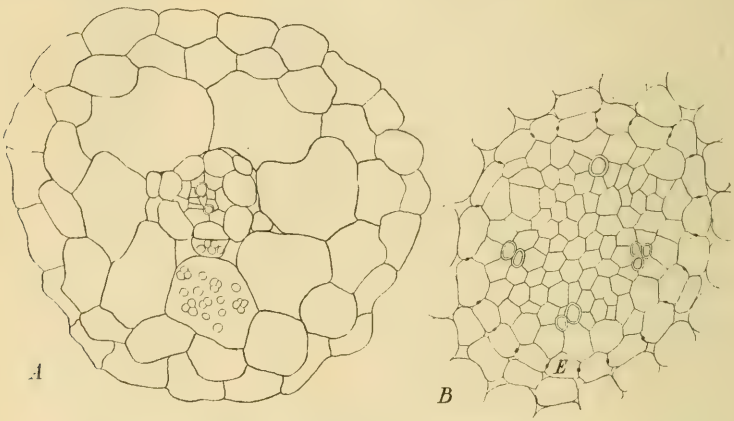

Fig. 3. *Primula egaliksensis.*

A, Tranverse section of the primary root (Seedling from the Botanical Garden, Copenhagen); (Obj. 4, Oc. 4). *B*, Transverse section of a young adventitious root, showing the central cylinder and the inner layers of the primary cortex; *E*, Endodermis with Casparian spots; (Obj. 4, Oc. 6). (Igaliko.)

vascular strands of the leaves, also a central group of 2—4 vascular bundles. Towards the upper end of the rhizome, where this passes over into the terminal peduncle, the number of the vascular bundles increases, but with a reduction in the size of each bundle, and at the same time several layers of the surrounding parenchyma develop into a continous sclerenchymaring. The vascular bundles differ from the normal and approximate to the hadro-centric type with sieve-tissue closing more or less distinct'y round the inner side of the bundle; exceptions to this are seen in the bundles at the

apex of the rhizome which are always distinctly collateral. These bundles („steles", v. Tieghem) are surrounded by sheaths having Casparian spots on the radial walls, and vary in shape from circular to oblong-arched. The walls of the parenchyma show pores, and its cells contained some starch (at end of July). In the proximity of the vascular bundles, the elements of the parenchyma are often arranged in fairly regular radial rows.

The Peduncle is provided with a 4—6-layered sclerenchyma-ring, which however is reduced to 3—4 layers opposite each of the vascular bundles; these latter are arranged in a regular circle. In a longitudinal section this sclerenchyma-ring appears to consist of elongated, cylindrical parenchymatous cells, densely and finely pored and with lignified walls. On the inner side of the ring, the sclerenchymatous tissue closely surrounds the leptome of the vascular bundles, thus affording some degree of protection. In the stereom, as well as in the medulla, near the vascular bundles, there are cells containing a brown substance, the nature of which, however, could not be further determined. Outside the sclerenchyma-ring the peduncle shows 4—6 layers of parenchymatous cells, lengthened axially and with large intercellular spaces communicating with the atmosphere through numerous stomates in the epidermis. Numerous chlorophyll granules are present in this parenchyma.

The pedicels attain a thickness of about 0.75 mm, and have on the whole the same anatomical structure as the peduncle.

The Leaf. The epidermal cells on the upper surface are larger and have thicker walls than those on the lower surface (fig. 4). The lateral walls are undulating, more so on the lower surface of the leaf. The outer walls show fine cuticular striations, especially near the margin of the leaf and above the midrib. The stomates are level with the surface

or slightly protruding; they are surrounded by 4 to 6 cells, most often 5. BØRGESEN states that the number of stomates is nearly equal on the upper and lower surfaces of the leaf, but such is not the case in the specimens of *Pr. egaliksensis*

Fig. 4. *Primula egaliksensis.*

a, The epidermis from the upper surface of the leaf. *b*, The epidermis from the lower surface of the leaf. (*a* and *b*, Obj. 4, Oc. 4). *c*, Transverse section of the leaf; on the lower surface a glandular hair; (Obj. 4, Oc. 6). (Igaliko.)

examined by me where the number of stomates was always greater on the lower surface.

The mesophyll (fig. 4, *c*) has a very lacunar structure, and palisade cells are scarcely distinguishable, though the

elements of the uppermost layer above the veins, are more elongated and cylindrical; the lower layers consist of slightly ramified cells. The whole of the mesophyll is rich in chlorophyll granules, which are also found in the epidermis of the lower surface.

Hydathodes are present on the leaf-margin, opposite the stronger veins. Small glandular hairs, with a one-celled

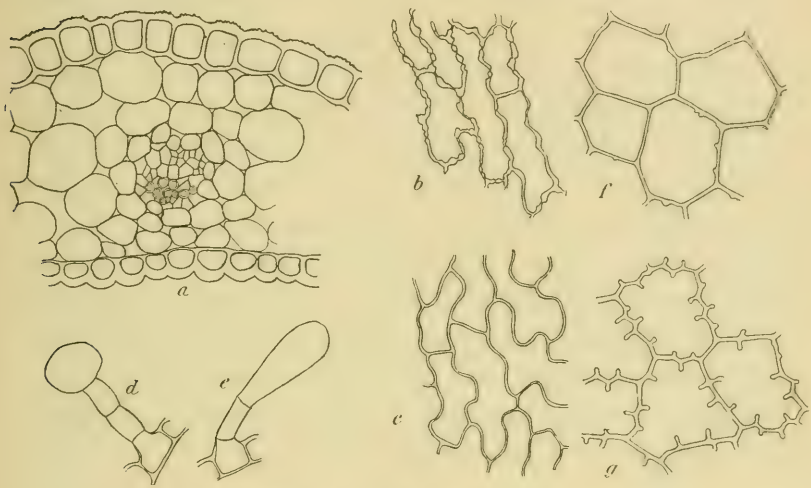

Fig. 5. *Primula egaliksensis.*

a, Transverse section of the calyx near its base. *b*, The epidermis from the inner surface of the calyx. *c*, The epidermis from the outer surface of the calyx (the apex of the lobes). (*a*, *b* and *c*, Obj. 4, Oc. 4). *d* and *e*, Forms of hairs from the margin of the calyx-lobes; (Obj. 4, Oc. 6). *f*, The epidermis from the upper surface of the corolla-limb. *g*, The epidermis from the lower surface of the corolla-limb; (Obj. 3, Oc. 12). (Igaliko.)

head on a one-celled stalk are found on both surfaces of the leaf, but only in small numbers. (Fig. 4, *c*.)

The Flower. The epidermis on the inner surface of the calyx, near its base, shows strongly thickened and arched cupola-like outer walls, the lateral walls being undulating and with irregular pores (fig. 5, *a* and *b*). Towards the apex the epidermal cells have more resemblance to those of the outer surface (fig. 5, *c*). Stomates appear fairly frequently on the outer surface of the calyx, being most numerous in the

somewhat depressed areas between the 5 chief veins; here the outer epidermal walls show fine cuticular striations. The margins of the calyx-lobes are covered with glandular hairs, the form of which is illustrated (fig. 5, *d* and *e*); the globular or club-shaped head is always filled with a brown substance. The cells of the mesophyll are somewhat axially elongated and are amply provided with chlorophyll granules, which also occur in the epidermis of the outer surface. There is a distinct difference between the epidermal cells on the upper and lower surface of the limb of the corolla. The outer walls of the upper side are strongly arched and papillose, with cuticular striations radiating from the top of each papilla. In the throat these papillae become very large, and their contents have here a strong brown colour. On the lower surface of the limb of the corolla, the epidermal cells are somewhat cupola-shaped, the lateral walls being provided with ridges at right angles to the outer walls (fig. 5, *g*). Similar ridges are also present in the epidermis of the upper surface, but much less pronounced in character, especially near the throat (fig. 5, *f*).

Primula sibirica Jacq.

Lit.: Flora Danica, t. 188 and t. 1809. Warming, 1886 a, pp. 25, 26, 27; 1886 b, p. 21. Widmer, 1891, p. 119. Decrock, 1901, p. 98. Pax and Knuth, 1905, pp. 76, 77. Blytt, 1906, p. 569.

Alcohol material, collected by E. Warming, from Norway, 1885 (Alten, Bosekop and Kåfjord). Herbarium material from the same places and also from Hammersfest (Vahl), the shores of the White Sea (Ångström 1843), Lapponia Imandrae (Brotherus, 1885) and Kola (Brotherus, 1889).

The following observations were made in addition to what is stated by Warming and Widmer as regards the morphology of *Primula sibirica*:

The leaves in the rosette appear to be arranged in a $\frac{3}{8}$ spiral, as is the case with *Pr. egaliksensis*, but 3—5 of the

embryonic leaves of the rejuvenation bud are developed as foliage-leaves during the summer. The succeeding leaves remain as scale-leaves, forming a protection for the young tissues of the bud, which in the following spring will develop into foliage-leaves, and terminate in the formation of the peduncle.

The duration of the adventitious roots is similar to that of the preceding species.

Apparently *Pr. sibirica* never developes more than one peduncle during one period of growth; at least, I have seen no specimens, which show indications of the autumnal rosette developing its peduncle during the same year as the parent-shoot.

The peduncle bears only a few flowers, and frequently only one of these attains to full development. But two subtending leaves at least are always present, and in the axil of the one which apparently bears no flower there is a microscopic rudiment of a flower-bud (fig. 6, *J*). Amongst the plants from Bosekop a few specimens were found to have four-partite flowers. The diameter of the limb of the corolla varies from 10—15 mm; the colour is a light lilac (Blytt), but according to Warming (1886 b) there is a white variety at Alten.

The biology of flower has been fully dealt with by E. Warming (1886, a, p. 27), who states as follows: "As regards the specimens from Alten, the following observations have been made: Normally developed, they are distinctly heterostylous, the figures showing the differences. According to my experience, the forms illustrated in fig. 8 (here reproduced as fig. 6) *C* and *D*, must be looked upon as the most common forms. In the long-styled flower the stigma is just in the mouth of the tube, level with the dark-yellow, wavy ring, which is present in this species as well as in *Pr. stricta* and other species. The very same differences known

in other heterostylous species are again met with here. The stigma of the short-styled flower is smaller, with smaller papillae, but the pollen-grains are larger (see fig. C^1). On the

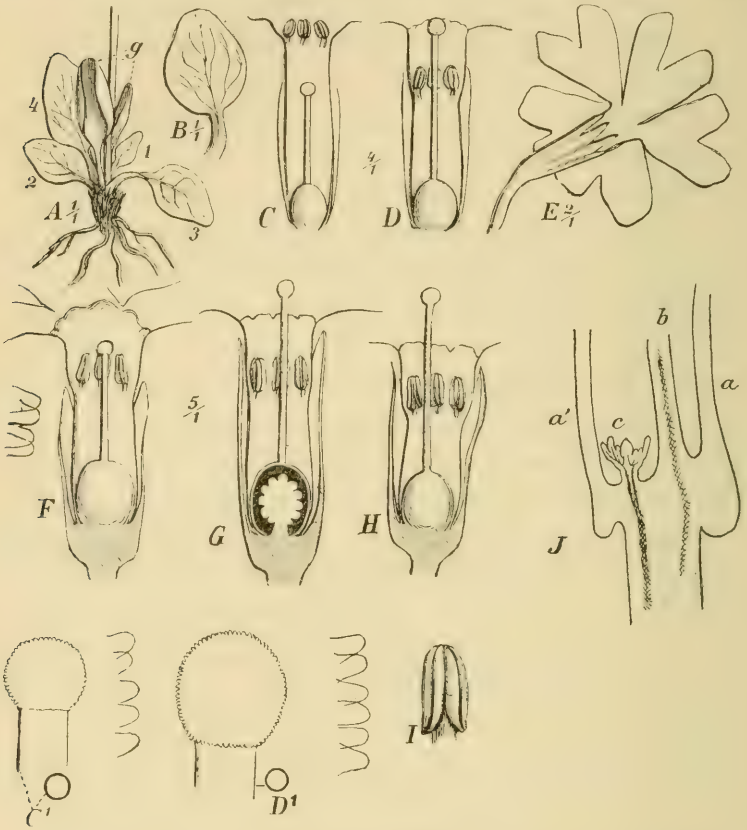

Fig. 6. *Primula sibirica.*

A, Base of plant in bloom, the foliage-leaves are marked in their order from below upwards, *1*, *2*, *3*, *4*; the uppermost, *4*, subtends the main bud, which has already developed *2* foliage-leaves (*g*). *B*, a foliage-leaf. *C*, short-styled flower. *D*, long-styled flower. C^1 and D^1, the corresponding stigmas, pollen-grains and stigma-papillae, in the same size, respectively. *E*, a long-styled flower, seen from behind. *F*, the stigma level with the distal parts of the anthers; the stigma papillae are illustrated to the left. *G*, a long-styled flower with much protruding style. *H*, a similar one, with still longer style. *I*, anther. *J*, longitudinal section through the distal part of the peduncle (10/1); *a* and *a'*, 2 subtending leaves; *b*, pedicel; *c*, a rudiment of the second flower. (Alten Fjord, Norway). (*A*—*I* from Warming 1886.)

other hand the stigma is larger in the long-styled species, the papillae are also larger, but the pollen-grains smaller (D^1).

Flowers are, however, also found, which have a relatively much larger pistil, with a stigma reaching above the limb of the corolla, for instance fig. *G*; I found the most protruding style in the flower illustrated in fig. *H*: the pistil is of about the same length as the one in fig. *G*, but the corolla tube is noticeably shorter, causing a larger portion of the style to protrude; the anthers in fig. *H* were not yet open. I have, however, never met with a short-styled flower, the anthers

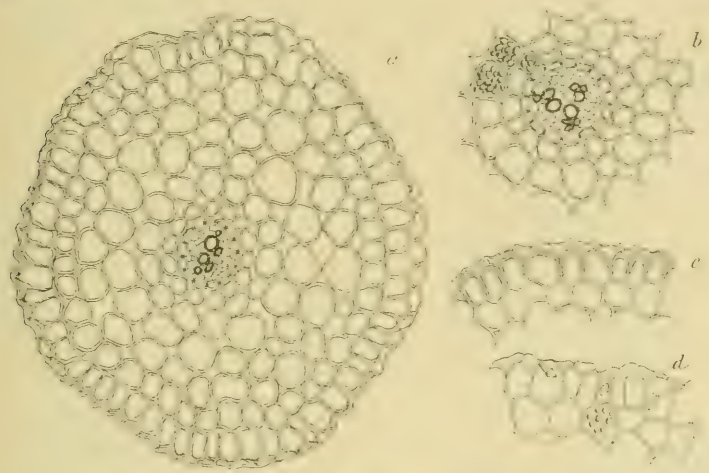

Fig. 7. *Primula sibirica.*

a, transverse section of a thin adventitious root. *b*, central cylinder with adjoining parenchyma of a 3-rayed adventitious root, some cortical cells showing contents of starch (*a* and *b*, obj. 8, oc. 6). *c*, the outer layers of the same root, greater enlargement (obj. 4, oc. 4) ; the section taken near the apex of the root. *d*, the epidermis and outer layers of the cortex of a root from the previous year (obj. 4, oc. 4). (Alten Fjord, Norway.)

of which corresponded in height with a stigma protruding to such extent. Finally, I have seen a plant at Kåfjord, with anthers and stigma at about the same level, as illustrated in fig. *F*; the calyx was here unusually short; the stigma was level with the tip of the anthers, showing its greater part above these; the anthers were open and full of pollen, and germinated pollen was found on the stigma. This was large and its papillae were in size just between those in the common long- and short-styled flowers (see fig. *F*, to

the left). This specimen was manifestly a self-pollinator, but this species is, on the whole, as eminently suited for cross-fertilization as our large flowered and dimorphic species."

Anatomy. Two-rayed adventitious roots occur (fig. 7, *a*), but the most common number of rays is 3 or 4. The epidermal cells perish quickly, but their outer, and especially their lateral walls are fairly resistant, so that well-preserved remains of the original outer layer may be seen even in older roots. On juvenile roots, the cortical cells have somewhat thickened walls (according to Decrock, a rather common feature of *Primula* species). Strong thickenings are especially noticeable on the outer and, in some measure, also on the lateral walls of the layer of cells, directly under the epidermis (fig. 7, *a* and *c*). These thickenings, consisting of cellulose, had disappeared in the root of the preceding year (fig. 7, *d*). The cells in the outermost layer of the primary cortex fit closely together and in close contact with the epidermis, their walls becoming somewhat cutinised with age. The young roots contain some starch in their cortical parenchyma. In the roots of the preceding year the starch was almost exhausted, probably during the spring growth, but I have found small single crystals of a calcium salt, especially in the exodermis (fig. *d*).

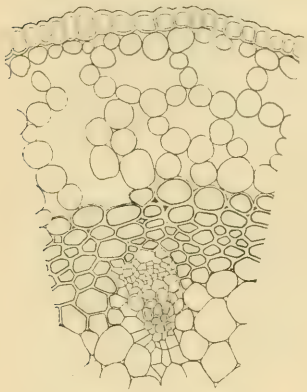

Fig. 8. *Primula sibirica.* Transverse section of a peduncle; the sector shows a vascular strand, stereome and assimilation-tissue, together with epidermis (obj. 4, oc. 4). (Alten Fjord, Norway.)

The rhizome has in all essentials the same structure as in *Pr. egaliksensis*, but both *Pr. sibirica* and the following species are characterized by having sclereids, singly or in small groups, in the medulla of the rhizome.

The transverse section of a peduncle (fig. 8) shows a structure somewhat less resistant than in the case of *Pr. egalik-sensis* and *Pr. stricta*. The assimilation tissue is more lacunar, and the stereome is provided with larger and less thick-walled elements. Chlorophyll granules are present also in the epidermis.

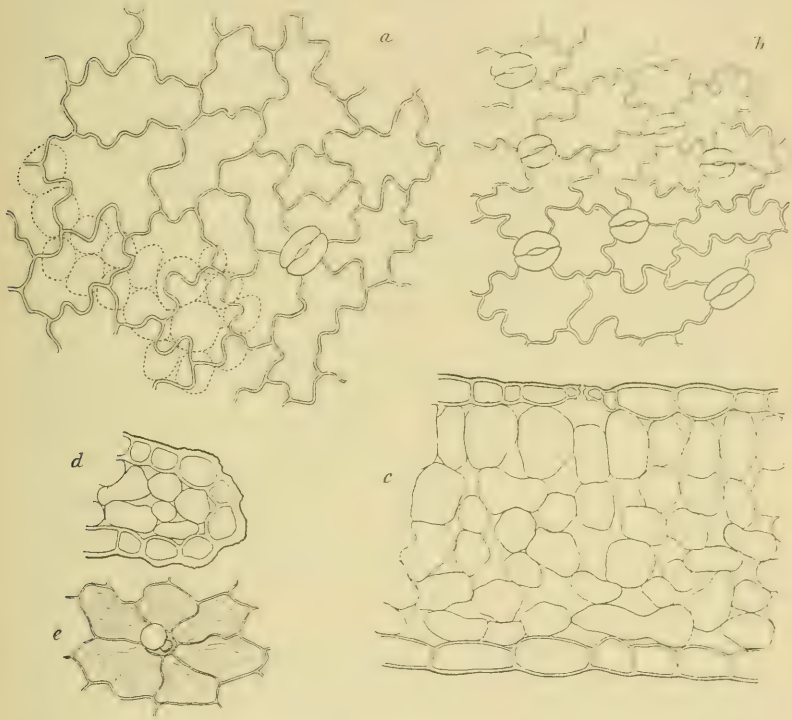

Fig. 9. *Primula sibirica.*

a, the epidermis of the upper surface of the leaf. *b*, the epidermis of the lower surface of the leaf. *c*, transverse section of the leaf. *d*, transverse section of the margin of the leaf. *e*, glandular hair from the upper surface of the leaf; the outer walls of the surrounding epidermis cells, with fine cuticular striations. (*a*, *b*, *c*, and *d*, obj. 4, oc. 4.) (Alten Fjord, Norway.)

The Leaf. The lateral walls of the epidermis on the upper surface show faint undulations, those of the lower surface being somewhat more pronounced (fig. 9, *a* and *b*). The outer walls are provided with fine cuticular striations (fig. 9, *e*) which are more strongly marked towards the margin of the leaf where the outer epidermal walls become thicker

(fig. 9, *d*). Both surfaces of the leaf are provided with stomates, the lower having by far the greater number; these are level with, or slightly raised above the surface, and are surrounded by 4—6, most frequently 5, cells. Glandular hairs of the usual Primula type are distributed fairly regularly, though very scantily, over the whole surface. A palisade layer is hardly distinguishable, though the cells of the corresponding layer are almost barrel-shaped (fig. 9, *c*). The mesophyll is, on the whole, very loose in structure, its bottom layer consisting slightly branched cells. It is amply provided with chlorophyll granules, and these are also found in the epidermis of both surfaces, although only scantily in that of the upper surface. Hydathodes are present on the leaf-margin opposite the stronger veins.

As in the case of the vegetative parts, the floral organs of *Pr. sibirica* differ only slightly from the corresponding parts of *Pr. egaliksensis*. The difference is limited to the less thickened outer and, especially, lateral walls of the epidermis on the inner side of the calyx (compare *Pr. egaliksensis* in fig. 5, *a*, *b* and *c*). The hairs, most often present on the margin of the sepals, are those with club-shaped heads.

Primula stricta Hornem.

Lit.: Flora Danica, t. 1385. Warming, 1886 a, p. 21 and the following; 1886 b, p. 7. Lindman, 1887, pp. 28, 77. Widmer, 1891, p. 122. Borgesen, 1895, pp. 223, 225, 229, 236, 237. Ekstam, 1897, pp. 166, 167. Pax and Knuth, 1905, p. 86. Sylvén, 1905, p. 125. Blytt, 1906, p. 568.

Alcohol material from the north of Norway (Bosekop near Alten Fjord, Kåfjord), collected by E. Warming, June 1885. Herbarium material from the same places, and also from Iceland (Restara, 1894, St. Stefansson) and Lapponia Imandrae (A. O. Kihlmann, 1892).

According to Sylvén, *Pr. stricta* shows, during its first stage of vegetative development, a great resemblance to the closely allied species *Pr. farinosa* and *Pr. scotica*. These latter develop

during the first summer a fairly dense rosette, and numerous adventitious roots arise from the base of the leaves, whereas the ramification of the main root is poor. The hibernation is effected by a winter-bud.

In the case of this species, it is not uncommon to find the same rhizome bearing several inflorescences during the summer. The rejuvenation shoot in the axil of the uppermost foliage leaf, as well as the augmentation shoots from buds in the axils of the lower leaves of the rhizome, are able to reach the flowering stage simultaneous with, or somewhat later than, the parent shoot.

The colour of the corolla is lilac with a yellowish throat-ring, the diameter of the limb being from 5—8 mm. Ekstam (p. 116) describes *Pr. stricta* as being scented, and states (p. 167): "während nur zwei, *Polemonium pulchellum* und *Pr. stricta* (mit starkem, unangenehmen Geruch, nach Kjellman), einen unangenehmen Geruch haben". Lindman ascribes to *Pr. stricta* "mycket stark, från lukt, lik den af orchisknölarna".

The morphology of the flower has been described by Warming (1886 a), and from this the following is quoted. "The Norwegian specimens (the author is comparing the details of *Pr. stricta* Hornem. with those of *Pr. stricta* var. *groenlandica* Warm. = *Pr. farinosa* var. *δ. groenlandica* (Warm.) Pax) are slightly protrandrous or perhaps sometimes homogamous. The anthers open very early and, as far as I have been able to see, most often somewhat before the stigma is fully ripe. Amongst the very numerous Scandinavian flowers, examined by me, I have found, but only in very few cases, the stigma in the precise relative position as in those from Greenland; the rule is, that the stigma protrudes more than in the latter; in some instances the stigma is found level with the tip of the anthers (fig. 10, *E*), while in others it is as much as 1 mm. above them (fig. *I*).

In the first case self-pollination may yet be possible and comparatively easy, while in the latter, it is rendered very difficult, or well nigh impossible, the flower being in an erect position all through. This greater length of the style is not caused by growth during flowering, as, in all the many specimens of buds examined, I have always found the same

Fig. 10 *A—D*, *Primula farinosa*, var. *groenlandica*, from Greenland (Itivnek near Holsteinsborg).

A, the whole plant and an isolated inflorescence, natural size. *B*, longitudinal section of a flower. *C*, the corolla-limb seen from above; the stigma surrounded by the anthers is seen through the throat ($^5/_1$). *D*, an anther.

E—F, *Primula stricta*, from Alten Fjord, Finmark.

E and *F*, longitudinal section of two flowers. *G*, the limb of the corolla, seen from above, ($^5/_1$). *H*, stigma and anthers are at the same level at *. *I*, longitudinal section of a long-styled flower. (From Warming 1886.)

relative lengths, the stigma being placed at a higher level, than in the specimens from Greenland. . . . . Only once I have found an inflorescence, the two flowers of which might

appear as being short-styled (fig. 10, *F*), and the flower illustrated in fig. *I*, when compared with this might be looked upon as the corresponding long-styled form; considering, however, that this fig. *I* depicts the longest styled flower I ever found, and that the length varies generally between that given in fig. *I* and in fig. *E*, while no flowers are found with the stigma below the anthers, I must look upon the form, illustrated in fig. *F*, as being accidental and of no great import."

To this I have only to add the following: Although the most common form amongst flowers from Norway is like that illustrated in fig. 10 *E*, yet it seems that long-styled flowers (as in fig. 10, *I*) are not so very rare. I have also found a few short-styled flowers (as in fig. 10, *F*). A difference was noted in the size of the stigma-papillae of the "long" and "short"-styled types, though this was certainly small. Flowers from Iceland all resemble the type in fig. 10, *E*.

The pedicel is lengthened a good deal after the flowering.

Anatomy. The adventitious roots are 4-rayed. The epidermis dies away quickly, and the protective function is transferred to the outermost layer of the primary cortex which becomes an exodermis, the cells of which are slightly cutinised on the outer and, to some extent, also on the lateral walls. Single crystals are frequent in the exodermal cells. Distinct Casparian spots occur on the radial walls of the fairly well-marked endodermis.

The more vigorous adventitious roots exhibit an incipient development towards the secondary type, in that the middle of the central cylinder is filled with hadromal elements, while the leptome groups increase in size; but no continuous cambium is formed, because the groups of meristematic cells situated between the protohadromal rays do not succeed in joining outside these. Young roots have the cortical cells filled with starch.

The rhizome quickly dies away from behind. A transverse section discloses the vascular bundles ("steles", v. TIEGHEM), circular to oblong-arched, surrounded by an endodermis, and resembling those of *Pr. egaliksensis* already described. Thick-walled and finely pitted sclereids appear both as groups in the medulla and isolated in the steles. The surrounding parenchyma

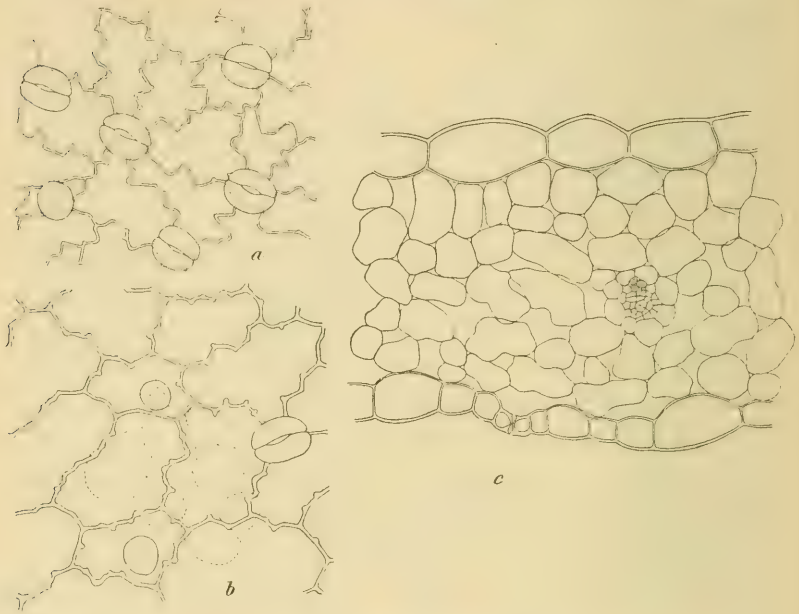

Fig. 11. *Primula stricta.*
a, the epidermis of the lower surface of the leaf. *b*, the epidermis of the upper surface. *c*, transverse section of the leaf, (*a*, *b*, and *c*, obj. 4, oc. 4). (Alten Fjord, Norway.)

has its adjacent cells arranged in radial rows, radiating from the vascular bundle; the cells are pitted and were found empty of starch (June, July).

The peduncle has the same structure as that of *Pr. egaliksensis.*

The Leaf (fig. 11). The lateral epidermal walls of the upper surface may be nearly straight or slightly undulating, while those of the lower surface are more strongly undulated.

The epidermal cells of both surfaces have their lateral walls strengthened by thickened bands at right angles to the surface; these originate fairly regularly from the convex side of the wall-foldings (fig. 11, *a* and *b*). Numerous cells with brown contents are found in the epidermis. Borgesen states that the number of stomates is somewhat larger on the upper than on the lower surface, but the opposite is the case in the leaves examined by me, where the larger number of stomates is on the lower surface. The stomates both on the upper and lower surfaces of the leaf, are most numerous towards the apex and near the margin. Glandular hairs occur evenly distributed, though rather scantily, over the whole surface of the leaf. As was the case with the two preceding species, the mesophyll is loose and little differentiated in structure (fig. 11, *c*). The uppermost layer consists of short, thick and often almost isodiametric cells; in the lowest layer the elements of the mesophyll become somewhat ramose and more horizontally elongated. Chlorophyll granules are plentiful throughout the mesophyll, and also in the epidermis of the lower surface, but they are few or entirely absent in that of the upper surface. Hydathodes are present on the margin of the leaf.

The floral parts are anatomically very similar to the corresponding parts of *Pr. sibirica*. The hair-covering of the calyx lobes consists principally of the type of glandular hairs illustrated in fig. 5, *e*.

Primula farinosa L., var. groenlandica (Warming) Pax.

Lit.: Lange, 1880, p. 70 (*Pr. stricta*); 1887, p. 260 (*Pr. stricta* var. *groenlandica*, Warming). E. Warming, 1886 a, p. 21 etc. (*Pr. stricta* var. *groenland.*). Rosenvinge, 1892, p. 683 (*Pr. farin.* var. *mistassinica* (Mich.) Pax). Abromeit, 1899, pp. 37—40 (*Pr. farin.* var. *mistassin.*). Pax and Knuth, 1905, p. 84.

Alcohol material from Itivnek near Holsteinborg (E. Warming, $^{24}/_{7}$ 1884). Herbarium material from Umanak, Strømfjord, Isortok and Itivnek in Greenland.

Pax and Knuth consider that the small *Primula* from Itivnek, described and illustrated by E. Warming (1886, a) belongs to the species *Pr. farinosa*, but as a special variety: *δ*, *groenlandica* (Warm.) Pax. The Greenland plants of this species differ from *Pr. stricta* Hornem., (which latter according to the above authors does not occur in Greenland; see also Rosenvinge), by having deeper incised corolla lobes, and by a calyx about the same length as the corolla tube, whereas in *Pr. stricta* the latter is considerably longer than the calyx (fig. 10). The relative length of the calyx tube and that of the corolla seems, however, to vary somewhat, not only in the true *Pr. stricta*, but also in the Greenland form of *Pr. farinosa*. No doubt, the plants from Itivnek have the calyx as long as the corolla tube, but, amongst about half a hundred specimens from various other places in Greenland, I found only a few flowers exhibiting similar proportions, the calyx being generally somewhat shorter. The same has been observed by Abromeit, who writes "die gelbe Kronröhre ragt etwa 2 mm aus den Kelch hervor". According to this author the pedicels increase greatly in length after flowering: "Die früher nur 2 mm langer Blütenstiele verlängen sich nach der Blütezeit bis zu 10 mm, und an einer alten abgestorbenen Fruchtdolde konnten gegen 24 mm lange Fruchtstiele gefunden werden". The deeply incised corolla lobes were found in all the specimens of this form, examined by me. Besides in South-West Greenland it also occurs in Labrador, thus sharing the same geographical area with *Pr. egaliksensis* (acc. to Pax and Knuth).

In vigorous specimens, the lower surface of the leaves is mealy (Abromeit, Rosenvinge).

The shoot-structure closely resembles that of the nearly related species already described.

E. Warming (1886, a) gives a description of the flower biology, and states in this connection: "All flowers from Greenland, examined by me, showed homogamy, as far as could be ascertained; in a bud, near its expansion, the pollen grains were observed lying loose and fully developed in the anthers still closed, and the papillae of the stigma were as large as those in an older flower; the stigma was in all species level with the middle of the anthers (fig. 10, *B*); self-pollination is inevitable as the corolla tube is very narrow, and the anthers lie close up to the stigma: the anthers incline somewhat towards the stigma (fig. 10, *B*), and looking into the throat from above, the stigma is found to be surrounded by the five anthers (fig. 10, *C*). Cross-pollination is of course not impossible, but it seems to me, that to be effective, the tubes of the foreign pollen must develop more quickly, than those of its own pollen. I found germinating pollen grains on the stigma, while pollen yet remained in the anthers". In all the flowers examined by me, I also observed, that the position of the stigma, in relation to the stamens, was as given in fig. 10, *B*. The limb of the corolla reaches a diameter of 8 mm.

As to the anatomy, this form corresponds so closely with the species described earlier, that a few remarks will suffice.

Crystals of a calcium salt were also found in the exodermis of the root of *Pr. farinosa* var. *groenl.* The sclerenchyma of the peduncle is only slightly developed in tiny specimens such as illustrated in fig. 10, *A*, but the plants may develop much more vigorously, and in these the structure of the peduncle is like that of *Pr. egaliksensis* and *Pr. stricta*. Abromeit states, that owing to the presence of anthocyanin in the epidermis, the peduncle, especially near its apex, also the pedicels and calyces, may be dark blue-black in colour.

The Leaf. The epidermis of the upper surface exhibits slightly undulated to nearly straight lateral walls, but those of the lower surface are strongly undulated. Thickenings of the lateral walls, similar to those in fig. 11 *a* and *b*, are also present, though less pronounced. No proper palisade layer is developed, nor in *Pr. farinosa* var. *groenl.* does the corresponding layer consist of the barrel-shaped cells, already described in the previous species. The bottom layer of the mesophyll has slightly branched cells. The mesophyll is liberally provided with chlorophyll granules, and these are also present in the epidermis of the lower surface. The number of stomates is, in this species, much greater on the lower than on the upper surface of the leaf.

Primula nivalis Pallas, var. *pumila* Ledeb.

Lit.: Kjellman 1882, p. 515; 1883, p. 492. Pax and Knuth, 1905, p. 102.

Herbarium material from arctic Siberia (Pitlekaj and the island of St. Lawrence) collected July 7th and August 1st, 1879, during the Vega expedition by Fr. R. Kjellman, and by him determined as being the variety *pumila* Ledeb. The chief difference from the main type, according to this author, lies in the almost entire leaves (1882, p. 515: "Mest afvika de med hänsyn till bladen, hvilka hos hufvudformen äro tätt och hvasst sågade, hos den arctiska formen åter alldeles helbräddade. Emellertid finnas öfvergångsformer"). In size they vary greatly; and Kjellman records finding specimens (St. Lawrence and Konyam bay), which, as regards vigorous development, were quite equal to the main type, wherefore he does not think that the designation *pumila* is quite appropriate.

My material consisted of specimens with peduncles measuring in height up to 10 cm, and the leaves attained to

5 cm long and 7—10 mm broad. The inflorescences vary up to 10 flowers.

In the monograph by Pax and Knuth, *Pr. nivalis* var. *pumila* Ledeb. is considered to be identical with Kjellman's species *Pr. Tschuktschorum* (1882, p. 516, t. IX), and the name *Pr. pumila* (Ledeb.) Pax, is consequently given to both. The description although it agrees closely with *Pr. T.* Kjellman, scarcely applies to *Pr. nivalis* f. *pumila* Ledeb. according to the material at my disposal here. This latter differs distinctly from the former in having broader leaves, and a longer corolla tube in proportion to the calyx. It also has, all over, a more vigorous habit, and the inflorescence is generally fuller. The two forms have the same area of distribution viz. north-eastern Siberia and the islands in the Behring Strait.

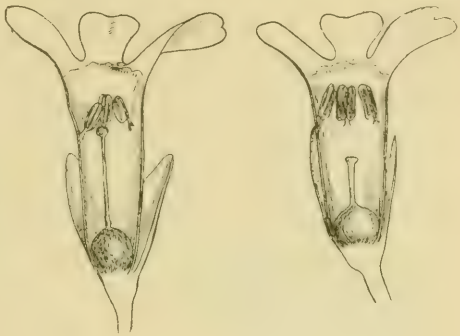

Fig. 12. *Primula nivalis* var. *pumila*. *A*, longitudinal section of a flower; the stigma is level with the base of the anthers. ($^3/_1$). *B*, longitudinal section of a short-styled flower, ($^3/_1$). (Pitlekaj.)

Kjellman gives (1883, p. 492, figg. pp. 490 and 491) the following description of the hibernation bud of *Pr. nivalis* from Chuckesland: "Det är, såsom synes, en mycket kraftig bildning. Dess längd är 35, dess tvärdiameter 15 mm. Dess hölja utgöras af ett antal kraftiga, tjocka lågblad, hvilka antagligen i viss mån bidraga till de inre delarnas skydd, men som derhjämta, och kanske huvudsakligen, tjenstgöra såsom förvaringsrum för upplagsnäring. Åtminstone äro deras parenchymcellar öfverfulla of stärkelse. Innanför dessa sitta knoppskottets assimileranda blad, — de äro stora

med tydligt urskiljbara delar, — och innerst sjelfa blomställningen, hvars hufvudaxel har en märkbar längd och hvars blomknopper äro fullt tydliga, ungefär 2,5 mm långa, och med alla blommans delar ganska långt utbildade . . .". In this *Primula*, the main bud also developes foliage leaves during the same summer, in which it is formed.

Flowers of type *A* (fig. 12) were found as frequently as of type *B*. The stigma in type *A* is level with the base of the anthers and self-pollination may thus readily be effected. Fig. 12, *B* shows a short-styled flower but corresponding long-styled form, which might be expected to be present, did not occur in the material examined by me. The stigma-papillae of *A* were slightly larger on the average, than those of *B*. The corolla is dark purple in colour.

Anatomy. The adventitious roots vary in thickness and in number of rays, and roots with 4, 5 and 6-rays were found. The endodermis is rather prominent, and Casparian spots are very distinct (fig. 13, *A*). The cells of the primary cortex were devoid of reserve-materials (July), and their walls showed collenchyma-like thickening. The epidermis is thin-walled and perishes quickly. The outermost layer of the primary cortex is developed as an exodermis, with the cells filled with a dark-brown substance.

The peduncle (fig. 13, *B*) differs from that of the species previously described by the absence of a sclerenchymatic ring during flowering. It appears, however, from a peduncle of the previous period of growth that the cells between, and just outside, the vascular bundles are somewhat thickened during the ripening of the fruits. Chlorophyll granules are present in the cells of the exceedingly lacunar cortex. The vessels in the strands are few and narrow (fig. 13, *B*), whereas the leptome is rather strongly developed. The parenchyma is thin-walled.

The leaf. The epidermal cells of the upper surface have straight lateral walls, or nearly so, which here and there are provided with flanged thickenings at right angles to the surface of the leaf (e. g. the two upper cells to the right, fig. 14, *a*). The outer-walls often have fine cuticular striations, especially on the epidermal cells over the midrib. The epidermis of the lower surface has undulating lateral walls,

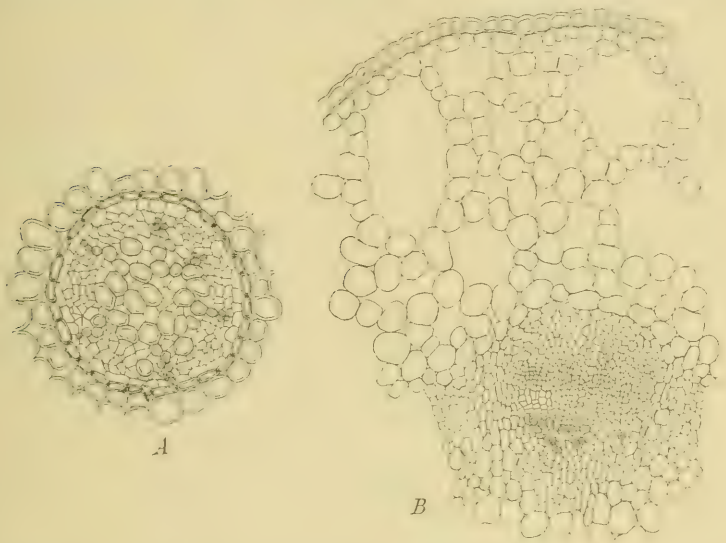

Fig. 13. *Primula nivalis* var. *pumila*.
A, the central cylinder and the adjoining tissues from a 6-rayed adventitious root; (obj. 8, oc. 6). *B*, the peduncle; the fig. shows a sector of the transverse section with a vascular bundle; (obj. 4, oc. 4). (Pitlekaj).

provided with thickenings similar to those already described for the upper surface; these are especially well-marked near the stomates (fig. 14, *b*). The stomates are exceedingly rare on the upper surface, whereas, on the lower surface, they are fairly numerous, from 90—110 per sq. mm; they are surrounded by 4 or 5 cells. Glandular hairs of the usual Primula type are present on both surfaces of the leaf, and they always originate from an epidermal cell much smaller than the surrounding ones (fig. 14, *a* and *b*). The

stomates are on a level with the surface of the leaf. Numerous cells, filled with a yellowish-brown substance, are present in the epidermis of both surfaces.

In this Primula the upper 1 or 2 layers of the mesophyll consist of elongated and closely placed cells, so that

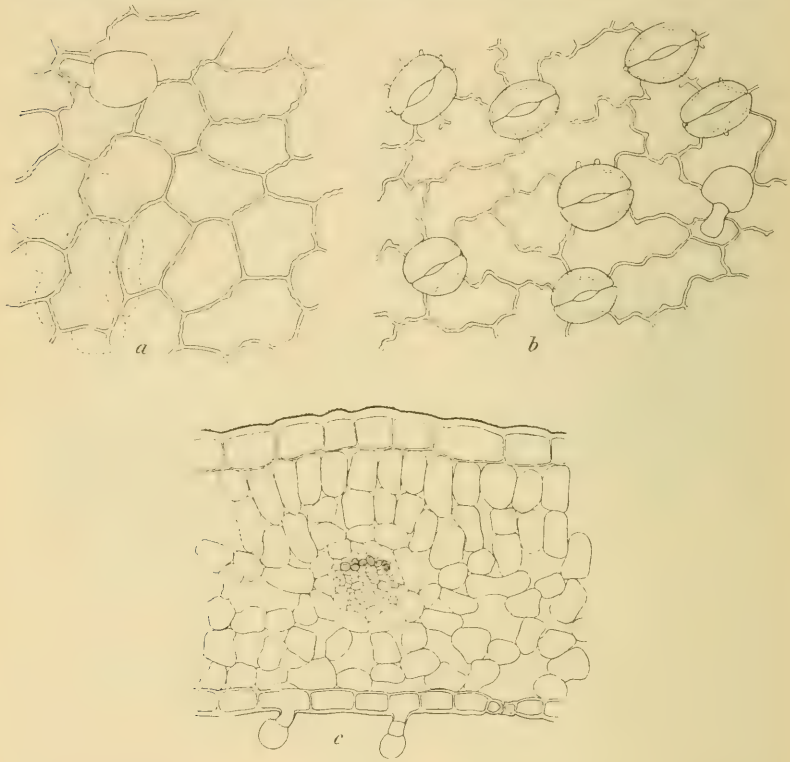

Fig. 14. *Primula nivalis* var. *pumila*.
a, the epidermis of the upper surface. *b*, the epidermis of the lower surface. *c*, transverse section of the leaf. (*a* and *b*, obj. 4, oc. 6; *c*, obj. 4, oc. 4). (Pitlekaj.)

they may be described as palisades (fig. 14, *c*). Towards the lower surface, the mesophyll becomes unusually lacunar, and consists of much branched cells extended in the plane of the leaf surface.

Androsaces septentrionalis L.

Lit.: Flora Danica, t. 7. Müller, 1881, p. 358. Brundin, 1898, pp. 24, 25, 27. P. Knuth, 1899, p. 307. Pax and Knuth,

1905, p. 214. Sylvén, 1905, p. 126. Blytt, 1906, p. 566. Ostenfeld, 1910, p. 61 (var. *Gormannii*).

Plants preserved in alcohol from Öland (E. Warming $^{31}/_{5}$ 1907). Herbarium material from Arctic Siberia (the mouth of the Lena River, 1883; Dr. Bunge), and Arctic America (King Point, A. H. Lindström, June 17th and 28th, 1906). The plants from the latter habitat belonged to *A. Gormannii* Greene, formerly considered a separate species, but the only difference from *A. sept.* is the shorter pedicels; Ostenfeld therefore ranks it with the latter species, but as a special variety (*A. septentrionalis* var. *Gormannii* (Greene) Ostf.).

A rosette plant of the *Draba verna* type (Brundin, Sylvén), generally appearing as a hapaxanthic winter annual, but sometimes it succeeds in attaining to pollacanthic growth (Sylvén, one specimen from Uppsala).

According to these authors, the seeds germinate at once during the summer, and a great number of leaves are developed before winter sets in. These remain green throughout the winter, except the lowest in the rosette, hence they can resume their assimilative functions in spring, as soon as conditions permit. No special bud-scales are provided for protecting the growing-point and the embryonic leaf-tissues against desiccation during the winter. The peculiar flat form of the rosettes is caused by the upper leaves growing more on the upper than on the lower surface, so that they are deflected downwards, pressing the lower and older leaves closely towards the substratum (Brundin). During the winter the leaves assume a deep red-brown colour (ibid.).

The primary root developes into a thin, slightly branched tap-root; adventitious roots do not occur.

The growth of the shoot terminates with a 7—10 flowered peduncle; weak specimens develop only one peduncle, whereas stronger ones produce several, through development of the axillary buds of the upper foliage-leaves; on a specimen from Boganida, I have found 19 peduncles, and *A. septentrionalis* is also depicted with several peduncles both

in Flora Danica and by Blytt. These secondary axes have often some foliage-leaves developed at their base.

Like other winter annual plants, *A. septentrionalis* is, according to Brundin, sometimes found flowering in the same year as it germinated.

The calyx is campanulate with 5 protruding ridges at its base, and its lobes reach somewhat above the corolla-tube. The diameter of the limb was found to be 6 mm on specimens from Öland, 3—5 mm on those from the Arctic; the limb and tube are white. In the throat of the corolla there are 5 projections, alternating with the corolla-lobes; they are sac-like expansions of the throat (fig. 15, *D*, shows part of the corolla seen from the outside). The centre of each projection is somewhat depressed (fig. 15, *A* and *E*). H. Müller remarks, concerning these throat-projections in *Androsaces* species, that they are yellow and often very conspicuous, and for this reason he thinks they are of importance as nectar contrivances; they are also useful in narrowing the throat, thus preventing drops of water from finding their way into the corolla tube, and moistening the reproductive organs. The uppermost flat part of the ovary functions as a nectary, and, according to the above author, a drop of honey is here secreted on dry and warm days.

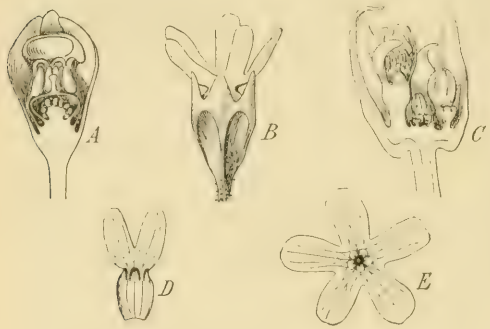

Fig. 15. *Androsaces septentrionalis.*

A, longitudinal section of flower-bud, ($^6/_1$). *B*, a recently opened flower, ($^5/_1$). *C*, a young inflorescence, developed from a bud in one of the uppermost leaf-axils of the rosette, ($^{10}/_1$). *D*, part of the corolla, seen from the outside; the limb is bent somewhat upwards, to show the throat-projections. *E*, the corolla, seen from above, ($^4/_1$). (Öland.)

H. Müller has found, by studying *A. septentrionalis* in the Alps, that visits by insects (various Diptera) are not frequent. The inflorescence, which consists of a few rather small and insignificant flowers, attracts but few visitors, hence he assumes, that the plant will often be dependent on self-pollination. The proximity of the stamens to the stigma (fig. 15, *A*) must greatly facilitate this.

Anatomy. In its anatomical structure, the root of *A. septentrionalis*, according to Decrock's description (p. 121),

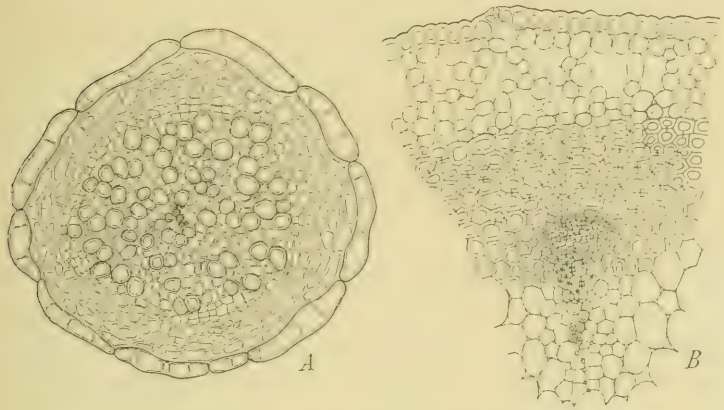

Fig. 16. *Androsaces septentrionalis.*
A, transverse section of a root-branch; (obj. 4, oc. 6). *B*, the peduncle; a sector of a transverse section with a vascular strand; (obj. 4, oc. 4). (Öland.)

seems to resemble closely that of *A. maxima*; no difference was found between the main and the secondary roots. The primary cortex is few layered and thin-walled, and perishes quickly, with the exception of the innermost layer, the endodermis. This consists of comparatively large cells, which, during the development of the root, divide by radial walls, so that the endodermis can keep pace with the considerable growth of the central cylinder (fig. 16, *A*); the outline of each original endodermal cell is marked by a cutinised lamella. The young root, provided with 2 hadromal rays, quickly attains the characteristics of the secondary type; the one

depicted (fig. 16, *A*) is thus only 0.5 mm thick; the parenchymatous ground tissue, surrounding the numerous vessels, is lignified at the periphery of the hadromal part. In the leptome the sieve tubes seem to be few, but their precise determination is made difficult by the rapid thickening of their lateral walls, which in a transverse section makes them resemble the somewhat collenchyma-like parenchyma cells surrounding them. In the periphery of the root, the parenchyma cells appear to be tangentially extended and are frequently divided by thinner radial walls.

The peduncle. A lacunar tissue of axially extended cells, containing chlorophyll granules, is surrounded by a thick, strongly cuticularised epidermis, provided with stomates (fig. 16, *B*); the peduncle is therefore, in this case, an organ with assimilative functions. Inside this tissue is seen a stereome including up to 10 layers of very elongated and thick-walled parenchymatous cells, with finely pitted lateral walls. The first-formed vessels (see fig. 16, *B*, below) are placed nearly in a radial line, and have only a few ill-defined annular thickenings, so that in the fully developed peduncle, they are found quite flattened by the turgid pressure of the surrounding tissue. The ground-tissue has very thin walls, and often perishes during the ripening of the fruit, when the peduncle becomes hollow.

The pedicels, about 0.5 mm thick, are very similar in structure to the peduncle.

The leaf. The epidermis of the upper surface (fig. 17, *A*) has straight, often pitted, lateral walls, those of the lower surface being rather strongly undulated (fig. 17, *B*). The outer walls show cuticular striations, especially distinct around the hairs. Of these two kinds are present: I. glandular hairs with a one-celled stalk (less frequently two-celled) and with a unicellular head; these originate from a cell which is smaller than the surrounding epidermal cells.

II. multicellular, thickwalled and most frequently branched cover-hairs with a warty cuticle; various forms are depicted in fig. 17, *D*, *E* and *F*; *D* and *E* showing the thickness of the walls. Stomates, surrounded by 4—5 cells, are present

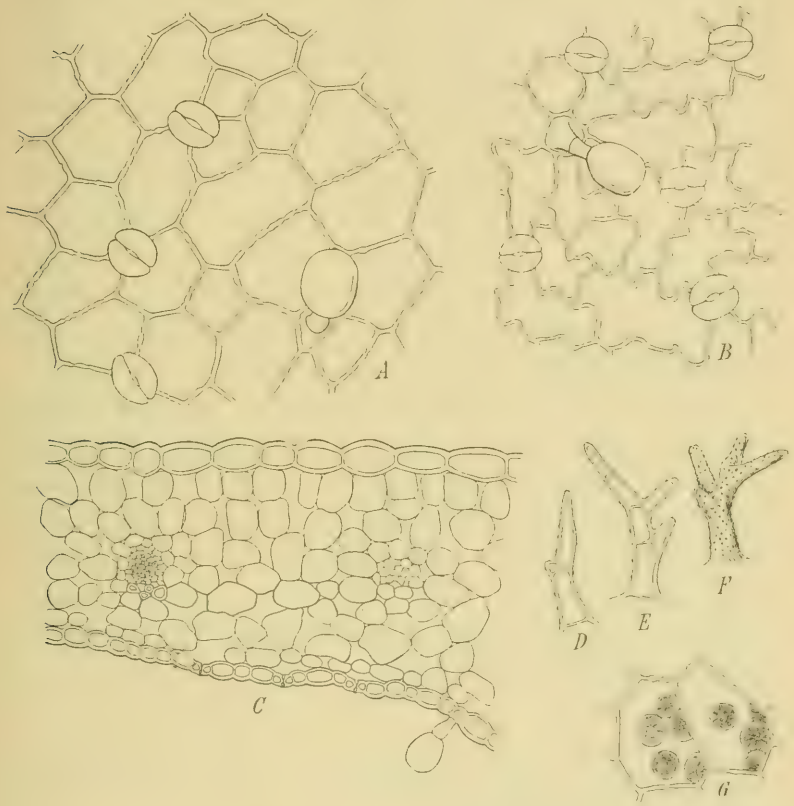

Fig. 17. *Androsaces septentrionalis.*
A, the epidermis of the upper surface of the leaf. *B*, the epidermis of the lower surface of the leaf. *C*, transverse section of the leaf; the vascular strand to the left shows collenchyma-like thickened tissue on the lower side. *D*, *E* and *F*, different forms of cover-hair; *D* and *E* are seen in optical section. *G*, epidermal cells from the upper surface of the leaf, with contents of spheroidal formations. (C, obj. 4, oc. 4; the rest, obj. 4, oc. 6.) (Öland.)

on both surfaces of the leaf, but there are about double as many on the lower than on the upper surface, the proportion varying only slightly in plants from different habitats.

The total number of stomates per leaf is, however, on an average far greater on specimens from Öland, than on those from Arctic America and Siberia.

The apex of the leaf and of each of the 2—4 teeth in its margin, are provided on the lower surface with a group of hydathodes, from which the distal portion of the veins extends fan-shaped as a well-developed epitheme.

A transverse section (Fig. 17, *C*) discloses from 2—4 layers (the thickness of the leaf is somewhat variable) of short and broad palisade cells, which like the rest of the mesophyll are rich in chlorophyll granules. The undermost layer of the mesophyll consists of rather strongly branched cells. Frequently the epidermis of the lower surface is found loosened from the mesophyll. The vascular bundles are sometimes accompanied by cells with collenchymatous thickening (fig. 17, *C*, the vascular bundle to the left). In the epidermis of both lower and upper surfaces, though most frequently in the latter, there are cells filled with a brown substance. In all the leaves examined by me, but only in the upper surface, this contains some peculiar spheroidal and deeply brown-coloured bodies (fig. 17, *G*), which were exceedingly resistant towards solvents; they may perhaps be only a precipitate caused by evaporation, or by preservation in alcohol.

With regard to the floral parts of *A. septentrionalis*, the calyx presents a peculiar anatomical structure, so that it deserves further attention.

A transverse section (fig. 18, *A*) of one of the 5 projecting ridges of the calyx (see p. 196) shows a layer of thin-walled cells within the epidermis of the outer surface of the calyx; these cells are in close contact with each other, and also with the epidermis without any intercellular spaces. This layer (probably an aqueous tissue) is seen in fig. 18, *B*, in surface-view; its elements appear very elongated, with

their ends wedged together, and they contain chlorophyll granules, like the mesophyll. The stomates are limited to the upper part of the calyx (i. e. the lobes and a narrow belt below these), and they are about equally numerous on both surfaces. The lateral walls of the epidermis are undulating, more especially on the inner surface of the calyx and also on the 5 concave depressions between the protruding parts of its outer surface; they are less strongly undulated, or nearly straight, on the protruding parts.

The limb of the corolla has papilla-like arched epidermal cells, which are most prominent on the upper surface, especially so round the throat-scales, but these, however, are not papillary. The flat polygonal cells, which cover the throat-scales, were filled with a brown substance.

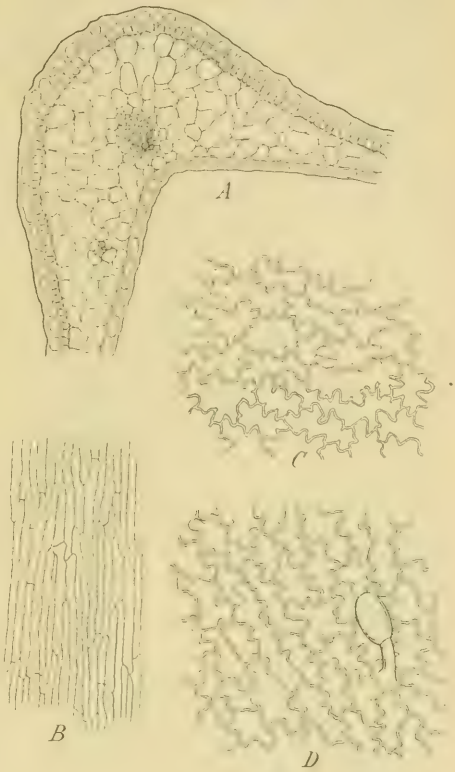

Fig. 18. *Androsaces septentrionalis.* *A*, transverse section of one of the protruding parts of the calyx; under the epidermis of the outer surface is seen a continuous layer of thin-walled cells. *B*, surface-view of this layer. *C*, the epidermis from the inner surface of the calyx. *D*, the epidermis from the outer surface. (*A*, *B*, *C* and *D*, obj. 8, oc. 6.) (Öland.)

Androsaces chamaejasme Host.

Lit.: Wydler, 1859, p. 22. Müller, 1881, pp. 358, 359. Holm, 1885, p. 44; tab. VIII. Eastwood, 1902, p. 211. Knuth 1899.

p. 307. Pax and Knuth, 1905, p. 188, etc. Ostenfeld, 1910, p. 61.

Alcohol material from Jugor Schar ($^{9}/_{9}$ 1882), collected by Th. Holm. Herbarium material from Arctic America (var. *arctica* Knuth, Herschell Island $^{13}/_{7}$ 1906, A. H. Lindström); Arctic Siberia (Chabarowa, August, 1894, H. Fisher; Wajgatsch, July, 1875, Fr. R. Kjellman and A. N. Lundström); also from Central Europe (the Alps, the Carpathians).

This plant developes long and short shoots alternately on the same axis (see fig. 19, *A*) and is similar to *A. lactea*, which is described by Wydler, as having the densely leaved rosettes separated by long-jointed internodes.

Fig. 19. *Androsaces chamaejasme.* *A*, a small specimen from Herschell Island, (see the text); the plant shows the withered remains of 4 peduncles, the one furthest to the left is the youngest, the middle one the oldest, ($^{2}/_{3}$). *B*, rosette with 3 rejuvenation buds, ($^{2}/_{1}$). *C*, rejuvenating shoot, where the change from long internodes to the densely leaved rosettes has taken place twice, ($^{2}/_{1}$). (*A* from Herschell Island, *B* and *C* from Wajgatsch.)

In the species here described, the peduncles are terminal (thus differing from *A. lactea*), the rejuvenescence must therefore be effected by means of axillary buds (fig. 19, *B*). During the summer in which the parent-shoot forms its peduncle, some of these buds develop into lateral shoots similar in structure to that of the parent-shoot. The length of the long-jointed internodes varies greatly, from 5 cm down to a few mm, and sometimes even less, so that the plant becomes almost cushion-like.

The rosettes are generally bent towards the ground, or even rest on this, in which case adventitious roots may develop, and facilitate the vegetative extension of the plant;

this development is however rare. The plant (from Herschell Island) depicted in fig. 19, *A*, has, however, a more erect growth, and this is the more characteristic form of specimens from this locality. There was a considerable amount of clay and sand amongst the withered leaves of the three lower rosettes (fig. 19, *A*), and it seems probable, that the plant has grown on a spot, where, under certain conditions, its vegetative organs were periodically covered by deposits, thus causing the plant to assume a more erect manner of growth, necessary for maintaining life.

The leaves do not seem to retain their assimilative function beyond one period of growth, and the leaves developed during the previous summer were nearly always withered before the following spring. The withered leaves are fairly resistant, and they may remain on the plant for several years before crumbling away.

Special bud-scales are not formed, but the young leaves, which are very hairy, especially on the margins, protect the growing point by bending across it. There are two fairly well differentiated types of axial shoots: one has a thicker elongated internode and a densely leaved rosette; the other has a thinner axis and fewer leaves in the rosette, and its growth never terminates by the development of a peduncle.

As regards the anatomy, there is a marked difference between the long-jointed internodes of these two types, which will be dealt with later.

The flower. The size of the corolla seems to vary greatly (fig. 20, *A* and *B*). I found it largest on plants from Herschell Island and from Wajgatsch, a diameter of 12 mm being attained; it was distinctly smaller (6—8 mm) on plants from other habitats. The colour is whitish-yellow, the 5 small projections narrowing the throat, having a more pronounced yellow colour. According to H. Müller, who thoroughly describes the biology, these throat-scales change their

colour and become red when the flower has reached the stage of pollination. This is effected either by insects (Lepidoptera, Hymenoptera and, especially, Diptera), or by self-pollination, in the absence of these. The limb of the corolla also assumes a faint pink colour. This difference in colour between younger and older flowers is presumed to be a signal to the more intelligent insects, that the older flowers have already been cleared of honey by earlier visitors, hence they avoid the red flowers, and the result for the plant is a more intensive utilisation of the visits by insects (H. Müller).

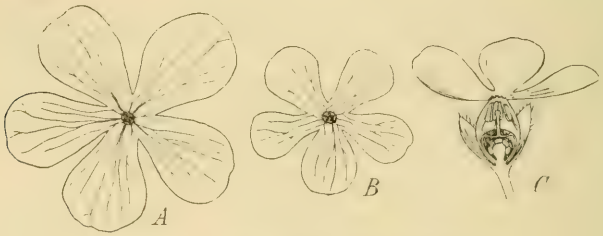

Fig. 20. *Androsaces chamaejasme.*
A and *B*, flowers seen from above; *A* from Herschell Island, *B* from Chabarowa, (5/2). *C*, flower, transverse section, (5/2).

Miss A. Eastwood mentions the change of colour in the corolla, so that it must also occur in arctic localities (Alaska).

Honey is secreted on the cup-shaped surface of the ovary (H. Müller).

Anatomy. An adventitious root, 0.5 mm in thickness, examined by me, was found to be 3-rayed, but had otherwise the same anatomical structure, as the root of *A. septentrionalis*.

The stem of *A. chamaejasme*, like that of other *Androsaces* species with a similar mode of growth [*A. lactea* (Wydler, 1859), *A. villosa* (Decrock, 1901)], shows a distinct difference as regards the structure of the naked long-shoots and the densely-leaved short-shoots.

As to the first, fig. 21 *A* illustrates a transverse section of a stem, which has carried a rosette with few leaves;

B and *C* show similar sections of the cortex and central cylinder, respectively, of a stem, where the rosette has been more densely leaved. Both have this in common, that the inner layers of the cortical parenchyma perish fairly quickly, except the endodermis which by division of its radial walls keeps pace with the growth of the central cylinder. The outer layers of the cortex acquire thickened and lignified walls, thus forming a continous

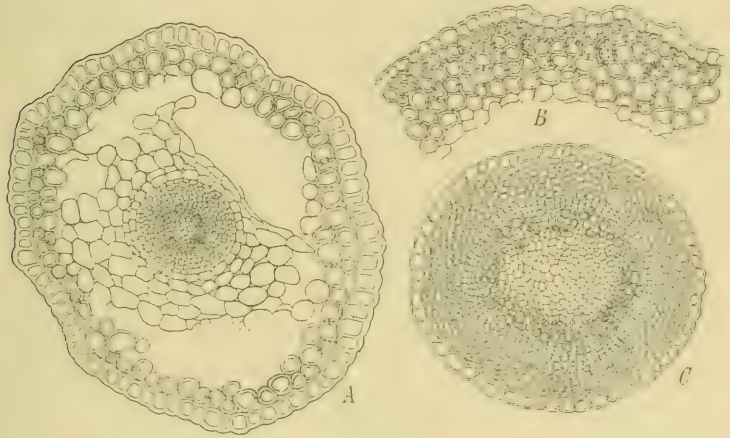

Fig. 21. *Androsaces chamaejasme.*
A, transverse section of a stem, which has borne a few-leaved rosette. *B* and *C*, respectively, the outer layers of the cortex with epidermis attached, and the centralcylinder with the endodermis of a stem with many-leaved rosette. (*A*, *B* and *C*, obj. 8, oc. 4.) (Jugor Schar.)

sclerenchymatic ring. By comparing fig. 21, *A* with fig. 21, *B* it is apparent, that the thickness of this ring differs in the two types of shoots; in *B*, 5—6 layers take part in the forming of the stereome, while in *A*, this only consists of 1—2 layers. When the shoots have reached a certain age, the central cylinder will be found lying free within a tubular sheath, formed by the lignified and thickened cortical parenchyma, together with the persistant epidermis filled with a brown secretion.

The cells of the cortical parenchyma are elongated axially,

and the elements of the external thickened layers are finely pitted, both in the end and the lateral walls. The central cylinder has a narrow medulla, surrounded by a continuous ring of vessels (fig. 21, *A* and *C*). A circular, continuous cambium commences its functions at a very early stage of the development, forming new vessels towards the centre. Outwards it forms sieve-tissue, the walls of which soon become somewhat thickened collenchyma-like, thus resembling, in a transverse section, the thick-walled parenchyma of the many-layered pericycle; in this, thin radial walls were noticed in a few of the cells (fig. 21, *C*).

The medulla becomes larger in the stem of the rosettes, and the continuous ring of vessels and sieve-tissue, present in the long internodes, is here interrupted by the leaf-traces inserted amongst them. The sclerenchyma in the periphery is here composed of much shorter elements.

The peduncle differs from that of the previous species, by having, most frequently, a somewhat less-developed stereome. It also has, like the calyx, long cover-hairs consisting of up to 7 thin-walled cells; in appearance they are minutely warted by cutinization. Glandular hairs with a 1—2-celled head on a 1—2-celled stalk, are also present.

The leaf. The epidermis has thin, undulating lateral walls; those of the upper surface are somewhat less undulated than those on the lower surface, though there is no great difference (fig.22, *A* and *B*). Glandular hairs, with a structure similar to those on the peduncle, are evenly distributed all over the surface. The cover-hairs are most numerous near the margin of the leaf; they are hyaline, 2—5 cells long, more or less thick-walled, and their surface is closely and minutely warted by cutinization; on the lamina of the leaf these hairs are few, and the short (2-celled) form is most frequent. The variety *arctica* Knuth (Herschell Island) is, however, distinguished by being closely covered with long

cover-hairs on both surfaces of the leaf. The epidermal cells from which the cover-hairs originate, are strongly arched. Stomates are present in great numbers on both surfaces. Where the leaves are pressed closely together in rosettes, the proportion between the number of stomates on the upper

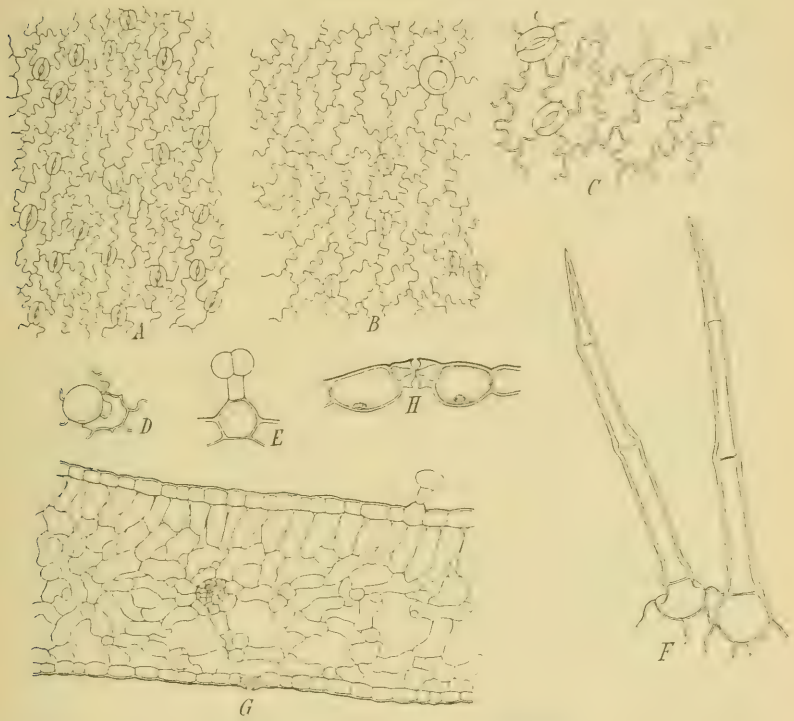

Fig. 22. *Androsaces chamaejasme.*

A, the epidermis of the lower surface of the leaf. *B*, the epidermis of the upper surface of the leaf. *C*, a piece of the epidermis, more enlarged. *D* and *E*, forms of glandular hairs. *F*, cover-hairs from the margin of the leaf, seen in optical section. *G*, transverse section of the leaf. *H*, a single stoma. (*A*, *B* and *G*, obj. 8, oc. 4; *F*, obj. 8, oc. 6; *C*, *D*, *E* and *H*, obj. 4, oc. 4.) (Jugor Schar.)

and lower surface is almost the same, but they are always somewhat more numerous on the lower surface. On shoots with few leaves (see fig. 19, *A*, furthest to the right), the stomates are much fewer on the upper than on the lower surface of the leaves; but, in this case the stomates are

more evenly distributed as compared with the densely leaved rosettes, where they are especially numerous towards the apex of the leaf. The total number of stomates per leaf seems generally greater on plants from Central Europe, than on those from the Arctic Zone.

In fig. 22, *G*, a transverse section of the leaf is given. The outer walls of the epidermis are only slightly thickened, and the stomates are either level with the surface of the leaf, or slightly raised above this. The illustration shows only one layer of palisades, but 2 and even 3 layers may occur (see Th. Holm, Tab. VIII, fig. 4). The aërenchyma is exceedingly lacunar in structure, and its cells are strongly branched.

Dodecatheon frigidum Cham. et Schlecht.

Lit.: Kjellman, 1883, p. 517. Eastwood, 1902, p. 211. Pax and Knuth, 1905, p. 239. Ostenfeld, 1910, p. 62.

Herbarium material from Arctic America (Port Clarence, 22nd and 26th July 1879, Fr. R. Kjellman; Herschell Island $^{13}/_{6}$ 1906, A. H. Lindström).

The geographical area of *Dodecatheon frigidum* seems to be fairly limited. With the exception of a couple of records in Oregon and Utah, which Pax and Knuth consider to be doubtful, it has only been found on the shores of Berings Straits and Alaska, and on adjacent islands. According to Kjellman, it grows chiefly amongst shrubs on mountain-slopes, but it may also be found on damp plains near the beach. The shoot-structure resembles that of the *Primula* species already described. The peduncle is terminal, and the bud, which is to continue the growth of the rhizome, developes in the axil of the uppermost foliage-leaf. In the material examined by me, were some specimens with an upward branching rhizome, which showed that the buds formed in the axils of the lower foliage-leaves may also attain to full development under favourable conditions.

The rhizome is closely covered with slightly branched adventitious roots, up to about 2 mm in thickness; both have a bright, brownish colour. The rhizome attains to a considerable length (up to 5 cm) by continuous annual growth, remaining alive for several years; on one rhizome I have counted up to 3 generations of shoots, plainly defined by the remains of the old peduncles. The withered bud-scales are found at the base of the spring rosettes, which consist of long-stalked ovate foliage-leaves 2—4 cm long, 0.7—2 cm broad. About the middle of July the hibernation buds are still small.

The peduncle carries 2—3 reddish-violet flowers, drooping when in full bloom.

The pollination process in species of *Dodecatheon*, according to KERNER (Pflanzenleben II p. 303), is as follows: The pollen-bearing insect, in search of honey, forces the cone-like column of anthers apart with its proboscis, and during this process part of the pollen falls out and becomes attached to the visitor. On the next flower visited by the insect, some of this pollen is left on the stigma and cross-fertilization is brought about. Should such fertilization not be effected, by the non-appearance of visiting insects, autogamy will take place. The short filaments become relaxed towards the end of flowering, and cause the anthers to separate somewhat, whereby the space inside the cone of anthers filled with pollen is opened, and the slightest shake causes the mealy pollen to fall on the stigma situated vertically below the anthers, because of the inverted position

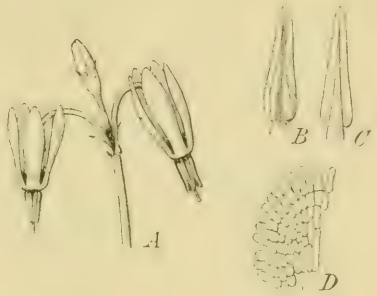

Fig. 23. *Dodecatheon frigidum.*
A, inflorescence (slightly reduced). *B*, an anther seen from the inside; the cavities of the anther are open. *C*, dorsal view of an anther, (*B* and *C*, $^3/_1$). *D*, the stigma papillae: (obj. 8, oc 4.) (Herschell Island.)

of the flowers (fig. 23, *A*). This figure also shows that the style of *D. frigidum* only reaches a few mm beyond the anthers. The papillae of the stigma are fairly long (fig. 23, *D*).

Anatomy. The adventitious roots are 3—5 rayed, with the central-cylinder surrounded by a strong endodermis (fig. 24, *B*). Some cells with thin walls occur scattered in this, especially opposite the hadromal rays. The primary cortex consists of a rather thickwalled parenchyma, of 16—20 layers. The outermost layer developes into an exodermis which in tangential section (fig. 24, *D*) shows both axially extended cells and short almost isodiametrical cells; these latter are comparatively thinwalled. The middle lamella is undulated, and in older roots (these alone were at my disposal) it is cutinised all round the cells, and this was also the case with the middle lamella of the endodermis. A transverse section of the outer layers of the root is illustrated in fig. 24, *C*; the fourth cell in the exodermis, from below, is one of the above-mentioned short and thin-walled cells; these are frequently filled with a brown coloured substance, similar to that which characterises the epidermis and the

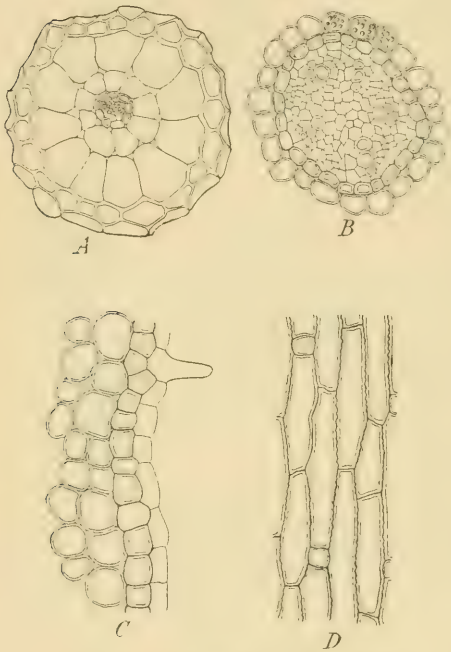

Fig. 24. *Dodecatheon frigidum.*
A, transverse section of a root-branch. *B*, the central-cylinder with endodermis and a layer of the surrounding cortical parenchyma of an adventitious root; the starch contents are shewn in some of the cells. *C*, the outer layers of the adventitious root. *D*, a tangential section of the exodermis. (*A*, *B*, *C* and *D*, obj. 4, oc. 4.) (Herschell Island.)

root-hairs. All the wall thickenings in the cortex consist of pure cellulose. It is possible, that the unthickened elements mentioned in the exo- and endodermis, have served as passage-cells for water at an earlier stage of the development of the roots, before the cutinization of the middle lamella reduced their permeability. The fact that the epidermis keeps alive and active as a water absorbing organ for a long time (I have found well preserved root-hairs nearly up to the base of the root), seems to me, at least, to confirm this supposition.

Fig. 24, *A* depicts a transverse section of a root-branch, about 0.5 mm thick; it is two-rayed and both endo- and exodermis are well developed.

The vascular bundles of the rhizome are arranged in a ring. The number varies somewhat according to the thickness of the rhizome, and I have counted up to 7 in a transverse section. In shape they vary from round to much elongated tangentially; anastomosis is frequent. They are collateral, and each is surrounded by a strand-sheath, with its cells often divided by thin radial walls. Outside the vascular-bundles, a "réseau radicifère" is formed (see Decrock p. 183 and 196), from which the adventitious roots initiate. The ground-tissue consists of fairly thick-walled, many-pitted cells, containing some starch (July). There was an active cork-cambium directly under the epidermis, on the part of the rhizome formed the previous year; the cells of the cork contained a brown substance.

The peduncle. The stereome, so common in the Primulaceae, is very slightly developed here; it encloses a circle of 15—20 vascular bundles, and to some extent, it surrounds each single strand. A quickly perishing ground tissue is present in the middle. Outside the stereome, an assimilative parenchyma with large intercellular spaces is

found. The epidermis is provided with stomates. Glandular hairs occur on the peduncle as well as on the pedicels (here particularly abundant), and on the calyx.

The leaf (fig. 25). The epidermis on both surfaces has undulating lateral walls. Stomates only occur on the lower surface, and are fairly evenly distributed, an

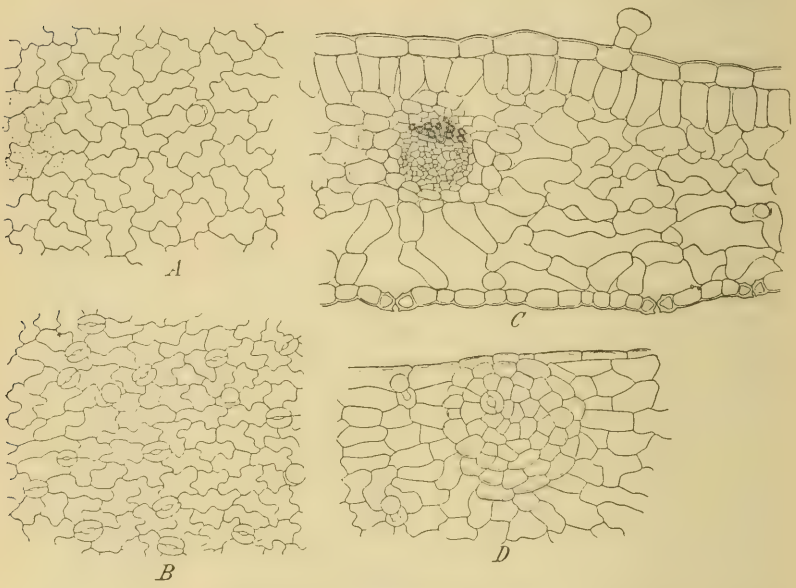

Fig. 25. *Dodecatheon frigidum.*

A, the epidermis of the upper surface; to the left the underlying palisade cells are drawn with dotted lines. *B*, the epidermis of the lower surface. *C*, transverse section of the leaf. *D*, a hydathode. (*A*, *B* and *D*, obj. 8, oc. 4; *C*, obj. 8, oc. 6.) (Herschell Island.)

average about 55 per sq. mm. Glandular hairs, with a unicellular, globular head on a 1-celled stalk, were present on both surfaces. The hydathodes are characteristic, each single water-pore (fig. 25, *D*) resting on a small wart-like base; they are situated on the upper surface of the leaf, near the margin and above the ends of the veins.

The transverse section (fig. 25, *C*) shows a single layer

of palisades and an aërenchyma with an exceedingly loose structure consisting of much-branched cells. Chlorophyll granules are plentiful throughout the mesophyll.

Summary.

A. **Growth forms**[1] and **shoot-formation.**

1. Chamaephytes: *Androsaces chamaejasme.*

A sedentary chamaephyte with a very persistent main root. When many leaf-rosettes are crowded together, *Androsaces chamaejasme* shows at times distinct transitions to the cushion-plant form. The adventitious roots appear very sparingly, hence vegetative propagation by root-forming rosettes can scarcely be of much importance. The foliage-leaves die in the autumn, except the innermost, partly expanded leaves. The withered leaves form a protection for the embryonic tissues of the axis, while the hair covering of the young leaves is most probably useful in the same way. The structure of the leaves is mesomorphic. The peduncle is terminal.

2. Hemicryptophytes: All the *Primula* species described above, and also *Dodecatheon frigidum.*

Perennial herbs with a quickly perishing main root, a vertical rhizome, and with leaves arranged in basal rosettes.

The rhizome of *Dodecatheon frigidum* reaches a comparatively considerable length, while the *Primulae* have only short ones, as they perish quickly from behind. The living part of the rhizome of the first four species described (viz. *Pr. egaliksensis*, *Pr. sibirica*, *Pr. stricta* and *Pr. farinosa* var. *groenlandica*) consists of a single year-growth only.

[1] C. Raunkiær: Planterigets Livsformer og deres Betydning for Geografien. København og Kristiania, 1907.

The main bud of the *Primula* species developes in the axil of the uppermost foliage-leaf, and generally produces a few leaved rosette, almost simultaneously with the flowering of the parent shoot. During the autumn some of the leaves remain in the scale-leaf stage, and as bud-scales form a protection for the embryonic tissues in the winter-bud. In spring these tissues develop into regular foliage-leaves (the spring-rosette) and the growth of the axis terminates with the formation of the peduncle.

Buds can, however, sometimes develop in the axils of other foliage-leaves, thus forming a "rhizoma multiceps". As adventitious roots develop in abundance, and (as mentioned above) the rhizome of the Primulas quickly perishes from behind, it is possible for vegetative propagation of these species to take place. A single individual may disintegrate into a larger or smaller group by the dissolution of the parts connecting the mother rhizome with its branches, so that the latter, by the development of adventitious roots, become independent plants.

The leaves have a mesomorphic structure.

3. *Androsaces septentrionalis* appears most frequently as a hapaxanthic winter-annual. The seeds germinate in the late summer, and before the approach of winter the plant has formed a small leaf-rosette, closely pressed towards the ground, and with a strongly developed main root. Bud-scales are not present, but the tip of the axis is protected by the half-developed innermost leaves of the rosette. During the spring following, the axis completes its growth by the development of a peduncle, and in the case of robust individuals, other flowering shoots are developed in several of the axils of the foliage-leaves.

The leaves developed during the autumn, hibernate and have a somewhat xeromorphic structure and appearance (the felted hair covering). Brundin states, that *Androsaces sep-*

tentrionalis, besides being a hapaxanthic winter-annual, may sometimes be seen to flower during the same year as germination has taken place (this is also the case with such plants as *Draba verna*); according to Sylvén it sometimes attains to pollacanthic growth. The plant seems thus to be somewhat variable as regards its growth-form. (Therophyte-Hemicryptophyte.)

B. **Flower Biology.** The nature of my material has prevented me from ascertaining, whether the inflorescence is formed during the year previous to its development, which is the case with numerous Arctic plants. According to Kjellman this takes place with *Pr. nivalis* (Arctic Siberia) and the same is most probably the case with the other Primula species described here, and perhaps also with *Dodecatheon frigidum*.

The *Primula* species, *Dodecatheon frigidum* and *Androsaces chamaejasme* have quite conspicuous flowers, those of *Androsaces septentrionalis* being less so. As to the colour of the corolla, this is reddish-violet to purple in *Pr. nivalis* and *Dodecatheon frigidum*, while *Pr. egaliksensis*, *Pr. sibirica*, *Pr. stricta* and *Pr. farinosa* v. *groenlandica* have a light purple to almost white corolla-limb with yellow throat-scales. The *Androsaces* species have white corollas with yellow throat-scales, but in *Andros. chamaej.* a change of colour takes place after fertilisation, the corolla then assuming a light purple colour. The uppermost flat part of the ovary serves as a nectary in the two species of *Androsaces*. The alpine Primulas, amongst others *Pr. farin.*, secrete honey from the wall of the ovary according H. Müller, but whether this is the case with the Arctic species, must remain an open question for the present.

Pr. stricta has a strong unpleasant scent.

As to dimorphism of the flowers, it can be stated, that *Pr. sibirica* appears to have a characteristic dimorphic heterostyled flower, with a very perceptible difference in size

between the stigma papillae and pollen granules of the short- and long-styled flowers. *Pr. egaliksensis* and *Pr. farin.* v. *groenlandica* have homomorphic flowers, the stigma being level with or slightly below the middle of the anthers. The flowers of *Pr. stricta* may perhaps generally be regarded as homomorphic, with the stigma placed a little above the anthers, but flowers are also found with the stigma raised considerably above the anthers, while others, have it situated much lower than the base of the anthers. Although I found a considerable number of flowers of *Pr. nivalis* with a very short style, the corresponding long-styled form seemed entirely lacking, and the greater part of the flowers examined had the stigma placed a trifle below the base of the anthers.

All species must be considered entomophilous; the *Androsaces* species are visited especially by Diptera (H. Müller).

Failing visits by insects, self fertilisation can probably take place without difficulty in the *Androsaces* species, *Pr. egaliksensis*, *Pr. farin.* v. *groenl.* and also in those flowers of *Pr. nivalis*, where the stigma is about level with the anthers.

C. **Anatomy.** I. According to their anatomical structure, the roots of the species examined can be classed into two groups, the first representing the mesomorphic, the second the more xeromorphic type (see Decrock).

1. The root of all the *Primula* species has a thin-walled and short-lived epidermis. Its protective function is assumed by the outermost layer of the primary cortex, the elements of which fit closely together, forming an exodermis, with the outer walls often slightly cutinised. The primary cortex is relatively an extensive tissue and, in *Pr. sibirica* and *Pr. nivalis*, its cells have somewhat thickened walls. An endodermis with Casparian spots can always be distinctly observed. The number of hadromal rays in the central

cylinder varies from 2 in the primary, and thin adventitious roots of *Pr. sibirica* to 6 (*Pr. nivalis*); 4 seems the usual number in the group Farinosae. The primary structure is retained throughout the existence of the root, though, in very strong roots of *Pr. stricta* I have found a few hadromal elements apparently of secondary origin. The primary cortex of the young roots is filled with starch, which is consumed during the spring growth. The adventitious roots of *Pr. egaliksensis*, *Pr. sibirica*, *Pr. stricta* and *Pr. farinosa* v. *groenl.* developed during the preceding summer, were found to die away; the primary cortical cells collapse and become empty, and in the case of *Pr. sibirica*, the thickenings of the cell walls disappear. In these roots of the preceding year, I have noticed diminutive crystals of a calcium salt, especially in the outer layer of the cortex; these were most frequent in *Pr. stricta*.

The anatomical structure of the root of *Dodecatheon frigidum* resembles most that of the Primulas. It differs in its characteristic exodermis and in the longevity of the epidermis. The number of hadromal rays in the adventitious roots varies from 3 to 5, but the finer lateral roots have only 2 rays. The cells of the primary cortex have somewhat thickened walls

2. In contrast to the type described above, the roots of *Androsaces* species pass quickly into the secondary stage. An active cambium ring is developed, and forms numerous vessels and wood-parenchyma toward the inside, and outwards leptome elements with somewhat collenchymatous thickened walls. The epidermis and primary cortex lying outside the endodermis, are thrown off. Through division along the radial walls, the cells of the endodermis are enabled to keep pace with the increase in thickness of the central cylinder.

II. All the species of the genus *Primula* described here are characterised by an anomalous structure of the rhiz-

ome (polystely and a "réseau radicifère"); polystely could not be proved in the case of *Dodecatheon frigidum*. These anomalies have already been thoroughly described by van Tieghem[1] and others for *Pr. nivalis*, *Pr. stricta*, *Pr. sibirica* and *Pr. farin*. Stone-cells, single or in small groups, are present in the medulla of *Pr. sibirica* and *Pr. stricta*, and the latter also has them enclosed in the individual steles. The cells of the ground-tissue are parenchymatic, coarsely pitted and contain starch. *Dodecatheon frigidum* has an active cork-cambium in the subepidermal layer of the cortex.

III. The vascular bundles of the peduncle and flower stalks are arranged in a regular circle. In most of the species they are surrounded by a sclerenchymatic ring (especially strong in *Androsaces sept.*); *Pr. nivalis* seems however to lack this stereome. A parenchymatic tissue is present outside the stereome; it consists of axially extended cells with large intercellular spaces, and is rich in chlorophyll granules. The epidermis is provided with stomates and covered with hairs of the same type as those present on the leaves of the respective species. The central ground-tissue consists of thin-walled cells, and is always homogeneous.

IV. The leaves of the *Primula* species, and those of *Dodecatheon frigidum* are provided on both surfaces, with glandular hairs of the usual Primula type (a unicellular head on a one-celled stalk). *Androsaces sept.* has in addition hairs with two-celled stalks, while in *Androsaces chamaejasme* the head of the glandular hairs may also be two-celled, the division being always effected by a central vertical wall.

The dense mealy covering, so characteristic for the

[1] van Tieghem: Struct. de la tige d. Primevères & Groupement d. Primevères, etc.; Bull. Soc. bot. de France, 1886. van Tieghem et Douliot: Polystélie; Ann. sc. nat. Ser. 7, T. III, 1886. For the literature of this subject see also Solereder: System. Anat. der Dicotyl.; Stuttgart, 1899.

lower surface of the leaves of many Primulas and which is known to be a resinous substance secreted from the head of the glandular hairs, is not met with, or only in a very limited degree, in the Arctic species closely related to *Pr. farinosa* (viz. *Pr. egaliksensis*, *Pr. stricta* and *Pr. sibirica*), but *Pr. farin.* v. *groenlandica* may have the leaves "mealy" on the lower surface, at least on vigorous specimens (ABROMEIT).

The leaves of the *Androsaces* species are covered with cover hairs, on the margins and the upper surface, those of *Androsaces sept.* being short and branched, while on *Androsaces chamaej.* they are long, hyaline and simple.

The lateral walls of the epidermal cells of *Pr. nivalis* and *Androsaces sept.* are straight or nearly so on the upper surface of the leaf; on the lower surface, however, they are undulating. The other *Primulae* and also *Dodecatheon frigidum* and *Androsaces chamaej.* have undulating lateral walls on both surfaces of the leaf. Fine cuticular striations were present on the outer walls of the cells of the genus *Primula* and also in the case of *Androsaces sept.*

Primula nivalis and *Dodecatheon frigidum* have stomates only on the lower surface of the leaves, but the other species are provided with stomates on both surfaces. *Pr. egaliksensis*, *Pr. sibirica*, *Pr. stricta*, *Pr. farin.* v. *groenl.* and *Androsaces sept.* have always by far the greater number on the lower surface. In *Androsaces chamaej.* the number of stomates on the upper and lower surfaces is almost the same, but only where the leaves are crowded together in dense rosettes, so that the stomates, on account of this, are mainly situated towards the apex of each leaf; where the leaves are arranged more favourably for development, as on the few-leaved shoots, then the stomates are much more numerous on the lower surface.

The stomates are level with the surface of the leaf, at times even somewhat raised above this.

The mesophyll is on the whole loose in structure. *Dodecatheon frigidum* has 1 layer, *Pr. nivalis* 1—2 and *Androsaces chamaej.* 1—3 layers of palisades. The leaves of *Androsaces sept.* vary somewhat in thickness, and show from 2—4 layers. The *Primula* species of the group Farinosae are characterised by having the uppermost layer of the mesophyll composed of somewhat irregular, ovate or barrel-shaped cells, with large intercellular spaces, so that a true palisade layer can scarcely be said to have developed. *Pr. farinosa* in the Alps shows, according to Wagner, the same peculiarity. In the case of *Androsaces chamaej.* and *Dodecatheon frigidum* the other layers of the mesophyll consist of richly branched cells, whereas in *Primula* species and *Androsaces sept.*, it is only in the lowest layer that the elements show any stellate ramification.

Chlorophyll is abundantly present throughout the mesophyll, and in special cases it was also found in the epidermis.

As is generally the case with Primulaceae, hydathodes are found at the tip of the leaves as well as on the margin opposite the stronger lateral veins.

Androsaces sept. has a small group of hydathodes at the tip of the leaves and also on the lower surface of each leaf-tooth; on *Dodecatheon frigidum* each hydathode is placed on a small, raised, wart-like base.

12.

A List of Arctic Caryophyllaceæ,

with some synonyms.

By

C. H. Ostenfeld.

1920.

1. **Moehringia lateriflora** (L.) Fenzl, Verbr. Alsin. tab. zu S. 18 (1833); *Arenaria l.* L. Sp. pl. 423 (1753).

2. **Merckia physodes** Fisch. ap. Cham. & Schlecht. in Linnæa I. 59 (1826); *Arenaria ph.* Fisch. in D.C. Prodr. I, 413 (1824).

3. **Arenaria ciliata** L. Sp. pl. 425 (1753).

1. subsp. **norvegica** (Gunn.) Fries, Mant. II, 34 (1839); *A. norvegica* Gunnerus, Fl. Norv. II, 144 (1772), tab. 9, fig. 7—9; *A. humifusa* Wahlenb., Fl. Lapp. 129 (1812); *A. ciliata*, β, *humifusa* Lange, Consp. Fl. Groenl. 27 (1880).

2. subsp. **pseudofrigida** Ostf. & Dahl, Nyt Magaz. Naturv. LV, 217 (1918).

4. **Stellaria media** (L.) Vill., Hist. pl. Dauph. III, 615 (1789); Lange, Consp. Fl. Groenl. 27 (1880).

5. **Stellaria longipes** Goldie, Edinb. Philisoph. Journ. VI, 327 (1822); Lange, Consp. Fl. Groenl. 29 (1880); *S. Edwardsii* R. Br., Chlor. Melvill. 13 (1823).

6. **Stellaria borealis** Bigel., Fl. Boston. ed. 2, 182 (1824); Lange, Consp. Fl. Groenl. 28 (1880); *S. alpestris* Hartm., Handb. Scand. Fl. ed. 2, 132 (1832); *S. calycantha* Bong., Veget. Ins. Sitcha 127 (1853).

7. **Stellaria humifusa** Rottb., Kiobenh. Selsk. Skrift. X, 447 (1770), tab. 4, fig. 14; Lange, Consp. Fl. Groenl. 28 (1880).

8. **Stellaria crassifolia** Ehrh., Hannov. Magaz. VIII, 116 (1784).

9. **Stellaria longifolia** Mühlenb. in Willd. Enum. Hort. Berol. 479 (1809).

10. **Stellaria graminea** L. Sp. pl. 422 (1753).

11. **Cerastium trigynum** Vill., Prosp. 48 (1779); Lange, Consp. Fl. Groenl. 30 (1880); *Stellaria cerastioides* L. Sp. pl. 422 (1753); *C. cerastioides* Britton, Mem. Torr. Bot. Club. V, 150 (1894); (?)*C. lapponicum* Crantz, Instit. II, 402 (1766); Lindman, Svensk Fanerog. Fl. 240 (1918).

12. **Cerastium nigrescens** Edmondston, Fl. of Shetland 29 (1845); *C. Edmondstonii* (Watson) Murb. & Ostf., Bot. Notis. 246 (1898); *C. latifolium* auctt., non L.; *C. latifolium*, β, *Edmondstonii* Watson, in Edmondston, Fl. of Shetland 29 (1845); *C. arcticum* Lange, Fl. Dan. Fasc. 50 (1880), tab. 2962, ex parte, non Lange, Consp. Fl. Groenl. 31 (1880).

13. **C. Regelii** Ostf., Vidensk. Selsk. Skr. Kristiania 1909, No. 8, 10 (1910); *C. alpinum*, γ, *cæspitosum* Malmgren, Spetsb. Fanerog. fl., Öfvers. Sv. Vet. Akad. Förh. Stockholm 242 (1862).

14. **C. alpinum** L. Sp. pl. 438 (1753); Lange, Consp. Fl. Groenl. 31 (1880).

var. **lanatum** (Lam.) Hegetschw., Reisen 154 (1825); *C. lanatum* Lam., Encyclop. I, 680 (1783—84).

var. **pulvinatum** Simmons, Sec. Arct. Exp. Fram 1898—1902 No. 2, 122 (1906); *C. alpinum*, var. *cæspitosum* auctt., non Malmgren.

subsp. **Fischerianum** (Ser.) Torr. & Gray, Fl. North Am. I, 188 (1838); Ostenfeld, Vidensk. Selsk. Skr. Kristiania 1909, No. 8, 39 (1910); *C. Fischerianum* Seringe, in D.C. Prodr. I, 419 (1824).

15. **Cerastium arvense** L. Sp. pl. 438 (1753); Lange, Consp. Fl. Groenl. II, 245 (1887).

16. **Cerastium cæspitosum** Gilib., Fl. Lithuan. V, 159 (1781); *C. vulgatum* L. Sp. pl. ed. 2, 267 (1762), non Fl.

Suecic. ed. 2 (1755), 158; *C. vulgare* Hartm., Handb. Scand. Fl. ed. 2, 182 (1820).

subsp. **fontanum** (Baumg.) Gürke, Pl. Eur. II, 223 (1899); *C. fontanum* Baumgarten, Stirp. Transilv. I, 425 (1816); *C. vulgatum*, **alpestre* Lindbl. in Fries, Summ. Veg. Scand. I 37 (1845); Lange, Consp. Fl. Groenl. 30 (1880); *C. vulgare*, subsp. *alpestre* Murb., Botan. Not., 253 (1898).

17. **Cerastium maximum** L. Sp. pl. 439 (1753).

18. **Honckenya peploides** (L.) Ehrh., Beitr. II, 181 (1788); *Arenaria p.* L. Sp. pl. 423 (1753); *Halianthus p.* Fries, Fl. Halland 75 (1817); *Ammodenia p.* Rupr., Fl. Samojed. cisural. 25 (1845).

var. **diffusa** (Hornem.); *Arenaria peploides diffusa* Hornem., Oecon. Plantel. ed. 3, 501 (1821); *Halianthus peploides* var. *diffusa* Lange, Comp. Fl. Groenl. 26 (1880).

19. **Minuartia verna** (L.) Hiern., Journ. of Bot. 37, 320 (1899); *Arenaria v.* L. Mant. I, 72 (1767); *Alsine verna* Wahlenb., Fl. Lapp. 129 (1812).

1. var. **hirta** (Wormsk.); *Alsine verna*, var. *hirta* Fenzl, in Ledeb. Fl. Ross. I, 349 (1842); *Arenaria hirta* Wormskiold, Fl. Dan. fasc. 28 (1819), tab. 1646; *Arenaria propinqua* Richardson, in Frankl. Journ. App. 17 (1823); *A. hirta*, β, *pubescens* Cham. & Schlecht., Linnæa I, 56 (1826); *Alsine verna*, γ, *hirta* et δ, *propinqua* Lange, Consp. Fl. Groenl. 24 (1880).

2. var. **rubella** (Wahlenb.); *Alsine rubella* Wahlenb. Fl. lapp. 128 (1812); *A. verna*, var. *rubella* Hartm., Scand. Fl. ed. 6, 149 (1854); *A. verna*, β, *rubella* Lange, Consp. Fl. Groenl. 24 (1880); *Arenaria hirta*, α, *glabrata* Cham. & Schlecht., Linnæa I, 56 (1826).

20. **Minuartia Rossii** (R. Br.) Graebn., in Ascherson & Graebner, Synops. Mitteleurop. Fl., Bd. V, 772 (1918); *Arenaria Rossii* R. Br., Chloris Melvill. 14 (1823); *Alsine R.*

Fenzl, Verbr. Alsin. tab. zu S. 18 (1833); Lange, Consp. Fl. Groenl. 25 (1880).

21. **Minuartia stricta** (Sw.) Hiern., Journ. of Bot. 37, 320 (1899); *Spergula stricta* Swartz, Vetensk. Akad. Handl., Stockholm, 20, 227 (1799); *Alsine s.* Wahlenb., Fl. lappon. 127 (1812); Lange, Consp. Fl. Groenl. 25 (1880).

22. **Minuartia arctica** (Stev.) Graebn., in Ascherson & Graebner, Synops. Mitteleurop. Fl., Bd. V, 772 (1918); *Arenaria arctica* Stev., in D.C. Prodr. I, 404 (1824).

23. **Minuartia macrocarpa** (Pursh) n. comb.; *Arenaria macrocarpa* Pursh, Fl. Am. Septentr. 1, 318 (1814); *Alsine m.* Fenzl, Verbr. Alsin., tab. zu S. 18 (1833); Ostenfeld, in Vid. Selsk. Skr. Kristiania, 1909, No. 8, 37 (1910).

24. **Minuartia biflora** (L.) Schinz & Thell., Bull. Herb. Boiss., 2 sér. VII, 403 (1907); *Stellaria biflora* L. Sp. pl. 422 (1753); *Alsine b.* Wahlenb., Fl. Lappon. 128 (1812); Lange, Consp. Fl. Groenl. 23 (1880).

25. **Minuartia groenlandica** (Retz.) n. comb.; *Stellaria groenlandica* Retz., Fl. Scand. ed. 2, 107 (1795); *Arenaria g.* Spreng., Syst. II, 402 (1825); *Alsine g.* Gray, Manuel, ed. 2, 58 (1856); Lange, Consp. Fl. Groenl. 26 (1880).

26. **Sagina cæspitosa** (J. Vahl) Lange, Tillæg No. 6 ad Rink, Grønland Bd. II, 33 (1857); Consp. Fl. Groenl. 22 (1880); *Spergula* (*Arenaria*) *cæspitosa* J. Vahl, Fl. Dan. fasc. 39 (1840), tab. 2289; ?*Spergula saginoides*, var. *nivalis* Lindbl., Physiogr. Sällsk. Skr. 328 (1837—38).

27. **Sagina intermedia** Fenzl, in Ledeb. Fl. Ross. I, 339 (1842); *S. nivalis* Lange, Consp. Fl. Groenl. 22 (1880), et auctt.; Fries, Mant. III, 31 (1842) ex parte.

28. **Sagina Linnæi** Presl, Reliq. Haenk. II, 14 (1831); Lange, Consp. Fl. Groenl. 21 (1880); *Spergula saginoides* L. Sp. pl. 441 (1753); *Sagina saginoides* Dalla Torre, Anl. Beob.

Alpenpfl. 189 (1882); *S. saxatilis* Wimm., Fl. Schles. 193 (1832).

29. **Sagina procumbens** L. Sp. pl. 128 (1753); Lange, Consp. Fl. Groenl. 21 (1880).

30. **Sagina nodosa** (L.) Fenzl, in Ledeb., Fl. Ross. I, 340 (1842); Lange, Consp. Fl. Groenl. 23 (1880); *Spergula nodosa* L. Sp. pl. 440 (1753).

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31. **Dianthus alpinus** L. Sp. pl., 412 (1753).

32. **Dianthus superbus** L. Sp. pl. ed. 2, 589 (1762).

33. **Silene acaulis** L. Sp. pl. ed. 2, 603 (1762); Lange, Consp. Fl. Groenl. 19 (1880).

34. **Silene tenuis** Willd., Enum. Hort. Berol. 474 (1809).

35. **Viscaria alpina** (L.) G. Don, Gen. Syst. I, 415 (1831); Lange, Consp. Fl. Groenl. 19 (1880); *Lychnis a.* L. Sp. pl. 436 (1753).

36. **Melandrium apetalum** (L.) Fenzl, in Ledeb., Fl. Ross. I, 326 (1842); Lange, Consp. Fl. Groenl. 19 (1880); *Lychnis apetala* L. Sp. pl. 437 (1753); *Wahlbergella a.* Fries, Summa Veg. Scand. 56 (1845).

37. **Melandrium affine** J. Vahl, Fl. Dan. fasc. 40, 5 (1843); *Lychnis aff.* J. Vahl, in Fries, Mant. III (1842); *M. involucratum* (Cham. & Schlecht.), β, *affine* Rohrbach, Linnæa 216 (1869); Lange, Consp. Fl. Groenl. 20 (1880); *Wahlbergella aff.* Fries, Summa Veget. Scand. 56 (1845).

38. **Melandrium triflorum** (R. Br.) J. Vahl, Fl. Dan. fasc. 40 (1843), tab. 2356; Lange, Consp. Fl. Groenl. 20 (1880); *Lychnis triflora* R. Br., in Ross, Voy. (1819).

13.

Caryophyllaceæ.

By

Eug. Warming.

1920.

As an introduction to my description of the morphology, anatomy and flower-biology of the Arctic *Caryophyllaceæ*, Professor C. H. Ostenfeld has kindly prepared the preceding systematic list of the species.

My description, which follows, is based: —

(1) On the investigations made in the Arctic Herbarium of the Botanical Museum of the University of Copenhagen, and on the alcohol material belonging to the same Museum, which has, in the course of years, been collected by the numerous Danish scientific expeditions to Greenland, (P. Eberlin, N. Hartz, Th. Holm, Chr. Kruuse, Andr. Lundager, C. H. Ostenfeld, L. Kolderup Rosenvinge, C. Ryder, Eug. Warming, etc.).

To this may be added some material which was collected in Iceland by Helgi Jónsson and C. H. Ostenfeld, and in Scandinavia (Finmark, Dovre, Finse) by Eug. Warming and others, and a small amount brought home by Swedish Expeditions to Spitzbergen.

(2) On the investigations and notes which I have made on living material in Greenland, Scandinavia and the Færöes.

(3) On the numerous notes found in the literature on the subject, especially in the Danish, Norwegian and Swedish. With regard to these notes the reader is referred to the list of literature at the end of this treatise.

I have divided the following description into four sections, viz.

I. Morphology and Vegetative Propagation.
II. Leaf Anatomy.
III. Adaptations to the Environments.
IV. Flower Biology and Notes on Seed-production.

I. Morphology and Vegetative Propagation.

According to the duration of life, and the forms of the vegetative shoots and the combinations of them, etc., I divide the species — for the sake of a general survey — into the following groups: —

A. The *Melandrium* type. Spot-bound,[1] pollacanthic, semi-rosette plants.

B. The *Silene acaulis* type. Spot-bound species, of which the long-shoots have short internodes, and narrow leaves.

C. The *Sagina nodosa* type. Spot-bound, pollacanthic species, with shoots which must be described as long-shoots with elongated internodes, although the basal leaf-pairs are close-set. Monopodial rosette shoot, at least in some of the species. No propagation by means of aërial runners.

D. The *Cerastium alpinum* type. Spot-bound, pollacanthic species, the shoots of which also usually have shorter internodes at the base, and must be called long-shoots, but which have terminal flowers (sympodia), and on which aërial runners are developed. Vegetative propagation can take place by means of layers.

E. The *Cerastium arvense* type. Species with shoots like those of D, but which have both aërial and subterranean runners, and a more constant vegetative propagation by means of runners.

[1] Spot-bound, that is, they have no horizontal shoots or runners, with which they can form "layers" (see Warming, 1884).

F. The *Stellaria crassifolia* type. Shoots like those of E, but with hibernacula.

G. The *Stellaria media* type. Hapaxanthic species.

It must be remarked, that there is absolutely no distinct limit between these groups — nor anywhere else in the plant-world — and it is possible that more exhaustive in-

Fig. 1. *Melandrium apetalum.*

vestigations will prove, that there are several more species with subterranean runners, than those quoted by me.

A. The Melandrium type.

Spot-bound, caespitose, pollacanthic species, with typical rosettes on semi-rosette shoots. The uppermost parts of the flowering shoots with elongated internodes usually protrude far above the rosettes (Fig. 1). No markedly pulvinate forms.

To this type belong the following *Sileneæ*: — *Melandrium affine*, *M. apetalum*, *M. triflorum*, *Viscaria alpina* and *Dianthus superbus*. Of non-Arctic: *Melandrium diurnum*, *Lychnis flos cuculi*, *Silene otites*, etc.

These are all perennial, usually vigorous herbs with a tap-root which remains during the whole life of the plant; but they are either devoid of or rarely provided with adventitious roots, which, when present, are insignificant. Vegetative propagation does not take place.

Fig. 2. *Melandrium apetalum* β *arcticum*. (Spitzbergen). *g*, Buds on the naked axis, either root-shoots or rather buds from the axils of rosette-leaves which have died and disappeared. *a*, Fragments of dead leaves. *b*—*e*, fresh leaves. Hairs omitted. (E. W.)

The larger the individuals are, the stronger is the tap-root, and the deeper does it grow down into the ground.

The shoots are semi-rosette-shoots, *i. e.* they have a typical rosette at their base, but otherwise have elongated internodes (long-shoots). The leaves are large when compared with those of the *Alsineæ*. Scale-leaves are absent. Lateral shoots, similar in structure to the main shoot, are developed from the axils of the rosette-leaves. All these shoots are erect or ascending. They are most frequently di-pleiocyclic, *i. e.* they remain 2—3 or more years in a vegetative stage, before their internodes elongate and flowers are developed; many undoubtedly remain throughout their

whole life in the vegetative stage. On an older plant the basal part is therefore composed of barren shoots (rosette-shoots) and of flowering shoots or the basal, dead portions of such shoots (Fig. 2), since at the commencement of the cold season, the shoots die so far down, that only small basal portions remain alive, which bear the buds for the next year. This results in a complex of shoots and portions of shoots which are held together by the tap-root and which have formerly been called "Rhizoma multiceps", "Radix multiceps" or, by Hj. Nilsson, "pseudorhizom", "Skott-basis-Komplex". In 1918 I suggested the old name "mesocormus" for it ("caudex", "Mellemstok", the French "souche").

Plants, with the structure described above, are typically cæspitose in habit (*plantæ cæspitosæ*), and occur singly, often growing scattered on the ground.

The flowering shoots can, in the same species, e. g. in *Melandrium triflorum*, be either very short or long (for instance 25 cm.) — according to the prevailing conditions.

The germination, in some of the species, has been investigated by Sylvén and Warming. The cotyledons are epigeous and resemble, more or less, the rosette-leaves (cfr. Figs. 5, 8). The first rosette is found immediately above the cotyledons. On cultivating *Viscaria alpina* I found no development of lateral shoots in the year in which it germinated, but in the second year lateral rosettes occurred, and already in these there were buds for the lateral shoots of the 3rd order. Three-year-old plants of this species were already in flower; but otherwise the number of years necessary for a plant to spend in a vegetative stage before it can flower, undoubtedly varies greatly, according to the prevailing conditions. In nature the vegetative stage appears to last for several years (Sylvén).

Melandrium apetalum agrees in its main points with *Viscaria* (Sylvén).

Winter-stage. All the buds are open, and the youngest foliage-leaves are protected during the winter by the older, withering leaves. How many of these remain green during the winter, depends evidently on the prevailing conditions, for instance, if the plants are snow-covered during the winter, or are uncovered and perhaps exposed to cold and desiccative winds. Statements made by botanists regarding the appearance of one and the same species during winter, therefore vary somewhat. As regards *Viscaria* I made the following note in West Greenland, on June 28th, at the beginning of spring: "passes the winter in a green condition". SYLVÉN (p. 291) says the rosette of the young plant passes through the winter "in an open rosette-stage". As regards *Melandrium apetalum* SYLVÉN says that the rosette-shoot of the young plant appears to pass through the winter in a more or less green condition, and regarding *Wahlbergella angustiflora* from Lapmark: the plants reared under cultivation remained green during the winter (p. 290).

Foliage leaves which have remained green during the winter, undoubtedly die immediately upon the commencement of the following spring. The old, dead leaves may persist for a long time, until they gradually disappear, the cold Arctic climate having no great putrefactive power.

Lateral shoots may be somewhat arching, or even slightly prostrate, at their base. This appears to be most decided in *Dianthus superbus* in which, from the mesocorm, there may proceed obliquely-placed branches with elongated internodes on which there may even occur, here and there, slender adventitious roots, but it appears to be absolutely certain that no vegetative propagation takes place. BLYTT (Norges Flora, p. 1073) mentions also these lateral shoots:

"numerous, short, sterile, leaf-bearing shoots," besides the "ascending or erect . . . stems." I have observed similar features in *Viscaria purpurea* (in Norway near Finse and in Denmark), and in *Viscaria alpina* there even appears to be an attempt towards the formation of scale-leaves on such shoots. In Denmark *Lychnis flos cuculi*, *Silene nutans* and *Melandrium dioecum* have similar shoots.

Pulvinate habit. Pulvinate forms develop easily from the typically cæspitose forms when the external conditions are unfavourable. When cold or strong wind checks the growth, the shoots become short and very much crowded, the entire mesocorm becomes very compact and closely set with branches, more or less semi-globular, and the flower-bearing portions of the shoots protrude only slightly above the surface of it. The pulvinate form is only a modification; to the same species may belong individuals with a divergently branched and long-branched mesocorm, and also dwarf-individuals with a pulvinate habit. The pulvinate form occurs at any rate in *Melandrium affine* and *apetalum*.

Adventitious Buds. On the naked vertical axis below the leaf-bearing mesocorm of old plants, small buds are sometimes seen, the origin of which may be doubtful (Fig. 2, *g*). Perhaps they are adventitious buds on the primary root, but it is more probable that they are axillary buds from former foliage-leaves on the main axis which buds have not had favourable conditions for their development. I have seen such buds in *Melandrium apetalum*, *M. affine* and *M. triflorum*.

B. The Silene acaulis type.

To this I refer only this one species, which is decidedly cæspitose in habit, and has a tap-root growing far down into the ground, but differs from the *Melandrium*-type in not having semi-rosette shoots, but long-shoots with short inter-

nodes. The primary root remains throughout the whole life of the plant, and can become very long. KRUUSE records the length as being 2 m, and SEIGNETTE almost 3 m.

The shoots may most properly be called long-shoots, and have close-set leaf-pairs, which do not cross each other at right angles, but grow in such a manner that, for instance, the 1st and the 4th leaf-pair stand perpendicularly above each other. Only a few (usually 4—5) fresh leaf-pairs occur simultaneously on each shoot, and these apparently form a small rosette at the end of the stem which is usually closely covered with old leaves and fragments of leaves (Fig. 3). The fresh leaves are immediately succeeded by the solitary, terminal flower (Fig. 3, *A*).

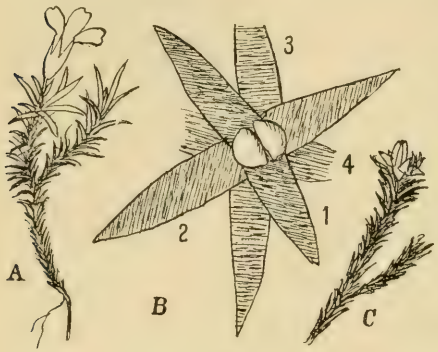

Fig. 3. *Silene acaulis*. *A*, A branch (Norway). *B*, The apex of a branch seen from above; the leaf-pairs, following each other in succession, are indicated by figures, and are, moreover, shaded in various ways. In the centre are seen two fresh, young foliage-leaves, not yet unfolded (Iceland; H. Jónsson, 26. 3. 1894). *C*, A branch from northern Sweden. (E. W.)

From the base of the tap-root, leaf-shoots proceed in all directions, which shoots are more or less branched, and are almost equal in height and are, moreover, almost always densely crowded, so that a flattened, semi-globular cushion is produced. SCHRÖTER (pp. 582 and 583) calls this form "Flachpolster." The branching of the shoots in the interior of the cushion is well-illustrated in Mrs. THEKLA RESVOLL's Fig. 36, p. 144; a compact tuft is shown "opened" and the branches are spread out. There are scarcely any of the Arctic Caryophyllaceæ which are so typically pulvinate

in habit as the present species. Many travellers have therefore described and illustrated these fresh-green, flatly-arched cushions, which during the flowering-period are covered with pink stars of 5 rays. Figures are found for instance in Bonnier, Lazniewski, Kerner (Pflanzenleben, Pl. 193), Börgesen (Botany of the Færöes), and in Feilden (Geog. Soc., April, 1898), C. Kruuse (1911, p. 358, Fig. 4) and others.

The shoots with their numerous old leaves, are usually so densely crowded in the cushions, that they form a spongy mass, which by its capillarity can absorb a great quantity of water. It is therefore very natural that adventitious roots are developed in their interior, which must to a certain degree take their nourishment from the old fragments of the plant's own leaves. But mention is also made of tolerably loose and divergently branched tufts, which may, for instance, have stems as long as 20 cm.; this is due to the nature of the station; as e. g. when the plant grows among damp moss, or in a particularly shady, damp locality.

Fig. 4. *Silene acaulis.* A small portion of a tuft; about $^1/_1$. On some of the shoots the green leaves are seen, surrounded by dead leaves. (From Iceland; Helgi Jónsson; 31. 12. 1893.)

Tufts, eroded by the wind, are described and figured by Hartz and Kruuse. Kruuse (1912, Fig. 41, p. 270) writes: "The tufts reach a diameter of 30—40 cm and a height of 7—10 cm, but the windward is often eroded and dead." Kihlmann also records such tufts from Kola.

Vegetative propagation under natural conditions is not known to me, but as gardeners are able to divide the tufts, adventitious roots must be so vigorously developed, that propagation by layers can take place.

Winter-stage. HELGI JÓNSSON (1895, pp. 279 and 285) has described and figured shoots in the winter-stage (l. c. Fig. 3, B, reproduced in this treatise as Fig. 4), and I have, in Fig. 3, B, given an illustration of the apex of a shoot in the winter-stage. Imbedded between the dead (shaded) leaves are seen two young, erect, conical, fresh-green leaves, which cover still younger leaves. But the features evidently vary, according to the prevailing conditions; on a specimen from a spot recently bared of snow (Upernivik, May 10th; C. Ryder) I observed pale, flabby, dead leaves at the apex of the shoots, but far down between them fresh leaves occurred, some of which contained starch, and also flower-buds were found (Fig. 24). HELGI JÓNSSON also found starch in the living leaves in winter time. KJELLMAN writes (according to citation in Sylvén, p. 287) regarding young plants under cultivation: "The plant passes through the winter in a green condition, and at the end of the winter, continues its development just where it was interrupted by the commencement of winter," and SYLVÉN himself says: "The plant seems to pass the winter in an open rosette-stage; the outer leaves, however, appear to become brown and withered at an early stage."

The seedling has, according to KJELLMAN (1901), an epicotyl-shoot with elongated internodes. He says that "*S. acaulis* under cultivation belongs to the type with elongated internodes." SYLVÉN mentions (p. 287) the young plants as remaining in nature in a rosette-stage during the three first years, but as distinctly, although only slightly, elongating their internodes during the following years. TH. RESVOLL (1917; p. 141, Fig. 36) also found that the seedling develops a leaf-rosette, which during the year of germination produces "as many as 3 shoot-generations of lateral branches." Not until the 3rd year did the first individual flower. It

consequently appears that the plant is on the point of transition to the semi-rosette stage.

Silene maritima, which so far belongs to the Arctic flora as it is found in Finmark and also in Iceland, appears to have exactly the same morphology as *S. venosa*, viz. a numerously branched mesocorm with erect long-shoots.

If any of the other species should be placed together with *Silene acaulis*, I believe it must be *Arenaria ciliata.*

C. The Sagina nodosa type.

To this group I refer *Minuartia biflora*, *M. arctica*, *M. hirta*, *M. groenlandica*, *M. macrocarpa*, *M. Rossii*, *M. stricta*, *M. verna* and the *Sagina*-species: *S. cæspitosa*, *S. intermedia*, *S. Linnæi*, *S. nodosa*, *S. procumbens*, and, for instance, the non-Arctic species, *S. saxatilis* and *S. subulata.* Arctic species, which I have not been able to investigate more closely, are *Alsine arctica* (Arctic America) and *A. macrocarpa.*

The above-mentioned species are generally low-growing plants, with the basal portions of the shoots close-set, and the flowering portions of the shoots protruding far outwards.

Primary root. Here also the primary root is, almost without exception (S. procumbens), the only root which is of any importance; it holds together the erect branches of the mesocorm. It remains during the whole life of the plant, and may be long, although it is most frequently slender, in accordance with the fact that the plants are small. Although adventitious roots may perhaps occur in all the species yet it appears that only in *S. procumbens* do they promote layering.

The characteristic feature in this group, when compared with all the others, as far as I have been able to see distinctly from the material to hand, is the fact that the primary

shoot is monopodial; indeed, it remains vegetative throughout the whole life of the plant, and the flowering shoots occur as lateral shoots of short duration, upon it and upon the other monopodial shoots developed as lateral branches. As the mesocorm is short and has very short internodes, it bears a rosette of foliage-leaves, and for lateral shoots it has partly flowering shoots, with elongated internodes, and partly new monopodial rosette-shoots. In the middle of the mesocorm of a plant of the above-mentioned species, we

Fig. 5. *Sagina nodosa.*
A, (about $^1/_2$). In August; I, primary shoot. *B*, Bulbil in the axil of a subtending leaf. *C*, In the axil of one of the lower-most pair of leaves there is only a bulbil, in that of the other there is a small shoot and a bulbil as an accessory shoot; likewise in all the following leaf-axils. The branches are arranged according to the usual, peculiar *Caryophyllaceæ*-mode of branching. *D*, Germinating bulbils (October). *E*, Seedling. *F*, A foliage-leaf. (Material from Denmark). (E. W.)

therefore always find a rosette, which is formed of narrow, linear leaves, and below this rosette there are often a great number of laterally placed, flowering shoots. These lateral flowering shoots may be most appropriately called semi-rosette shoots. A specimen of such a plant is seen in the accompanying figure (Fig. 5) of *Sagina nodosa.*

A monopodial primary shoot and monopodial shoots of

higher order are also found in *Sagina procumbens* and *S. subulata*, but hardly in all the *Sagina*-species; I do not think they are found in *S. apetala* for instance, nor in every species of *Minuartia*. It is often difficult to decide the exact condition, especially if the material to hand is not good. It is very desirable that the above-named and other species should be thoroughly investigated.

In monopodial species a terminal flower has exceptionally been found on the main axis, but it expands later than does the first flower on the lateral axes (Irmisch, Wydler). The monopodial structure has been treated of by the following authors: Al. Braun (Flora, 1843); Irmisch (1848, pp. 529 and 561; Bot. Ztg., 1850, p. 297); Wydler (Flora, 1851, p. 328; 1859, p. 314); Godron (Flore de France, vol. 1, p. 245).

The leaf-pairs in the rosettes alternate with each other at acute angles, so that, for instance, first the 4th or 5th leaf-pair stands under the 1st.

The flowering lateral shoots appear, as a rule, to last for two years only (this was observed in *Minuartia biflora*, *groenlandica* and *verna*), but cases in which they last a longer time may undoubtedly occur.

In addition to the flowering lateral shoots, sterile monopodial shoots, like the primary axis, may also be developed. Sometimes, some of these become prostrate, for instance in *Sagina nodosa*, *S. procumbens*, *S. Linnæi*, *Minuartia biflora* and *M. verna*, and may then strike roots. With this there occurs a possibility for the formation of layers, and this may happen, at any rate in the non-Arctic *Sagina subulata*. As regards *Minuartia biflora* and *verna* Thekla Resvoll states decidedly that she has not observed vegetative propagation; but it is possible that this may take place once in a way in *M. verna*. In *Sagina procumbens*, on the other

hand, vegetative propagation undoubtedly takes place by means of its rooting aërial shoots. To a certain degree it merits a special place, side by side with the *Stellaria*-type.

Sagina nodosa has a peculiar mode of propagation. In the axils of the foliage-leaves small, few-leaved shoots are developed (see Fig. 5): these shoots fall off and, on striking roots, form new individuals. For further details the reader is referred to the explanation of Fig. 5.

The Seedlings of *Sagina nodosa* immediately develop a rosette-shoot which sometimes forms branches during the first year. Its first internodes, however, are sometimes elongated (Fig. 5, *E*). In plants of *Minuartia stricta*, cultivated by me, small tufted plants were developed in the course of two months, lateral shoots with short internodes being quickly developed in some of the leaf-axils. In *M. biflora* THEKLA RESVOLL also found lateral shoots (Fig. 32), but SYLVÉN found none (loc. cit., p. 304). In other respects the seedlings of *Sagina Linnæi*, *Minuartia verna* and *M. intermedia* appear to correspond with those of *M. stricta* and *Sagina nodosa* (see Sylvén, p. 266 and Thekla Resvoll, Fig. 29).

As regards the time preceding the first flowering period THEKLA RESVOLL states, that it is not probable that *Sagina intermedia* flowers until the third year, but that *Minuartia verna*, when cultivated, had flowered in the 3rd year, and even in the 2nd year though sparingly, and that seedlings of *M. biflora*, when cultivated, flowered in the 3rd year; but, according to SYLVÉN, it appears that in nature the first vegetative-stage ("Forstærknings-Stadium") lasts for several years. It seems evident that the length of time is dependent on the prevailing conditions.

Pulvinate forms. The above-mentioned species are plants with a tufted habit, which may sometimes form dense

cushions. In the same species the branch-systems may either be long and divergently placed, with flowers raised high above the ground, or they may be so short and crowded together that dense semi-globular or globular cushions are formed with flowers, lying almost upon the surface of the cushion, or resting upon it. In Fig. 6 three specimens are shown which belong to the form-cycle of *Minuartia verna*, and

Fig. 6. *Minuartia verna* (reduced).
A, var. *hirta*. W. Greenland, 74°18′ N. lat. (C. Ryder). *B*, var. *hirta*. Scoresby Sound (N. Hartz). *C*, var. *rubella*. Spitzbergen (Hanna Resvoll Holmsen).

which show all these modifications within the same species. It is evident that the forms are dependent on the life-conditions prevailing in the stations.

A pulvinate habit has been found to occur in *Minuartia verna* (Fig. 6), *M. biflora*, *M. Rossii* (Fig. 7), *Sagina Linnæi*, *S. cæspitosa*, *S. intermedia* and *S. procumbens* (as also in *S. subulata*). See figures in Simmons, Pl. 6, pp. 4—6 and in Ostenfeld and Lundager, p. 19. In his excellent

treatise "Das Pflanzenleben der Alpen" C. SCHRÖTER (pp. 569—584) has given an account (accompanied by several figures) of plants with a pulvinate habit, and on p. 579 he has figured a cushion of *Alsine* (*Minuartia*) *sedoides*; he

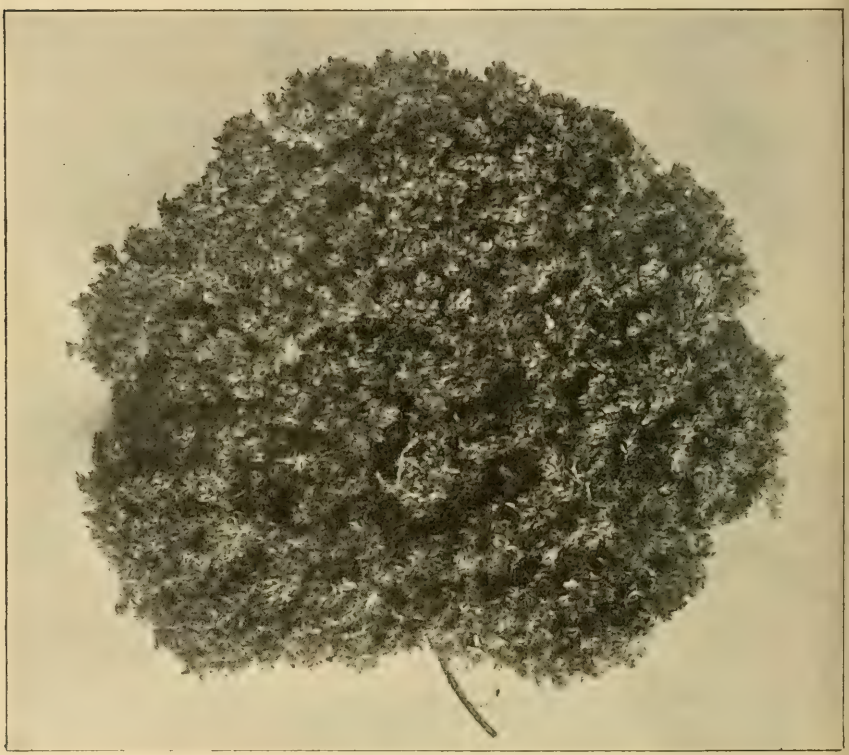

Fig. 7. *Minuartia Rossii.*
(Dragon Point; 21. 7. 1916; Thorild Wulff). A cushion seen from above. At the bottom the primary root is seen to protrude.

describes it as "halbkugelige Polster vom kahlem Azorella-Typus mit völlig glatter Oberfläche" . . . "Die Früchtchen sind in das Polster eingesenkt," etc. The species "gehört zu den letzten Pionieren der Vegetation."

The Arctic cushions may be fairly flattened and carpet-

like, without, however, being in reality "wandering." Slender, adventitious roots may occur in the interior of the cushions.

The Winter-stage. The same is the case here as in all the other Arctic Caryophyllaceæ: the buds are open; in the autumn there are fresh, green leaves, but during the winter many, or we may say, the majority of them, wither; nevertheless, the species may be called evergreen. At the commencement of spring, or of the time for the opening of the buds, the remaining leaves wither quickly. The degree of greenness of the plant is dependent on the station, especially if this is snow-covered or not.

D. The Cerastium alpinum type.

To this may be referred: *Cerastium alpinum*, *C. cæspitosum*, *C. nigrescens*, *C. Regelii* and *Arenaria ciliata.*

These also are typically spot-bound species, but there are no monopodial shoots, these being now if anything long-shoots with elongated internodes, even if the prevailing conditions may sometimes produce semi-rosette-like forms. Here also the internodes are shortest at the base of the shoots, and as branches arise more particularly from the base, mesocorms of the usual type are developed; the barren or flowering branches are held together by the primary root which remains during the whole life of the plant, but the branches of the mesocorm are not particularly close-set, and the basal shoots are often lying immediately upon the ground, spread out in all directions (cf. Fig. 9). This is probably an instance of psychrokliny, i. e. the direction of the stems is induced by the low temperature in accordance with Voechting's view. Added to this, the ground may possibly have been damp and this may have produced root-development; the pressure of the snow covering may also have had a part in it.

Adventitious roots are frequently developed on the prostrate shoots, but vegetative propagation does not take place, or rarely does so, through their agency.

Here also the habit of the plant is properly speaking tufted; to what a high degree the length of the shoots is dependent on the prevailing conditions, is evident from SYLVÉN's observations (*Cerastium alpinum*, pp. 299 and 300).

Fig. 8. *Cerastium alpinum.*
A, Young plant (from cultivation); about $^1/_1$. *B*, Basal portion of the cotyledons; buds are seen in both axils. *C*, Older plant (from cultivation; the internodes are less elongated than in *A*; after the cotyledons, the typical Caryophyllaceæ-branching appears, first with a vigorous shoot in the axil of the one leaf and a less vigorous in that of the opposite leaf, then with bud only in one of the axils of the two opposite leaves; in *A*—*C* the hairs are omitted. *D*, A leaf with its covering of hairs. *E*, Young shoot in spring. *F*, From N. E. Greenland; winter-stage, 21. 5. 1908 (A. Lundager). A pair of leaves with axillary shoot; there are no winter-buds nor any special covering for the buds. *G*, Branch of *Cerastium alpinum* γ *cæspitosum* (from E. Greenland). Secondary roots are developed; the hairs are omitted. (E. W.)

In nature the young plants appear to pass the winter "in a rosette-like-stage," he has, however, found the form *glabra* to develop in the first year" directly elongated internodes." The young plants which had been reared under cultivation

had, on the other hand, an elongated, richly-branching and plagiotropic epicotyl-shoot." This was also the case with the young plants reared by me under cultivation (Fig. 8)

The commonly occurring Arctic species *Cerastium alpinum*, which varies exceedingly in colour and hairiness, may serve as a type. It may in certain conditions form very

A *B*

Fig. 9. *Cerastium alpinum.*
A, From W. Greenland, 29th July, 1884. *B*, f. *pulvinata.* From E. Greenland, 25th Aug., 1900. (Hartz and Kruuse).

dense cushions, with short flowering shoots; but long, erect shoots, as much as 25 cm in length, may also be developed from the mesocorm (Fig. 9).

Cerastium nigrescens appears to behave like *C. alpinum*. It may be divergently branched, with long, erect shoots — and this is the rule — or it may be densely branched, even

— in rare cases — so densely, that it becomes somewhat pulvinate.

C. caespitosum with its variety *alpestre* varies in the same manner as *C. alpinum* (Sylvén, p. 300). It has sometimes very long stems. *Cerastium Regelii* I have only seen divergently branched.

At the apex of the shoots a kind of rosette is often met with, in that the internodes here are short temporarily, and a kind of winter-bud is developed, as for instance in *Cerastium alpinum*; the youngest leaves and flower-buds of the latter must thereby and by means of the densely villous-haired leaves be provided with an excellent winter-covering (Fig. 8, F). It is not always that such a shoot-development appears.

Similar features are met with in *Arenaria ciliata*. The stems with elongated internodes may be erect, but may also be more or less prostrate and entangled, covered with white flowers. Pulvinate forms may develop, although not so decidedly as in the *Minuartia*'s and in *Silene*. In other respects, it most resembles the latter in the form of its branches and the position of its flowers. It may have several (apparently lateral) flowers upwards along a long axis. I regard this as a sympodium, but have observed cases which were doubtful.

Vegetative propagation it appears does not generally take place. Neither THEKLA RESVOLL nor I have observed such in *C. alpinum*, although this species may have adventitious roots (Fig. 8, *G*). SYLVÉN, however, mentions "subterranean runners with scale-leaves (or scale-foliage-leaves)" in *C. alpinum*. Nor has THEKLA RESVOLL found vegetative propagation to take place in *C. nigrescens* (*C. Edmonstonii*).

The seedlings. SYLVÉN found that seedlings of *Cerastium alpinum* when growing in nature hardly flowered "until after the lapse of 2 years." The seedlings of *Arenaria*

ciliata β *norvegia* developed in Lappmark, in the year in which they germinated epicotyl-shoots with long internodes which often branched in the first year, but not until after the lapse of some years did they flower. Also under cultivation by me, they branched very soon.

Pulvinate forms. It is evident from what has been said regarding the form of the shoots, that there are not

Fig. 10. *Cerastium alpinum.*
The youngest part of the shoots are densely covered with woolly hairs. (From Iceland; Helgi Jónsson; 16. 1. 1894.)

such good conditions for the development of a pulvinate habit as in the first three types. It does occur however (Fig. 9). *Cerastium caespitosum* has been found in East Greenand with globular cushions, and Porsild (Medd. om Grönl., vol. 50, p. 370, Fig. 12) has figured a form regarding which he says "it differs greatly from the numerous forms of the species;" "especially distinctive is the low, densely-tufted growth, and the glabrous, obtuse, rosette leaves, etc." There is also mention of dense tufts in *Cerastium nigrescens*, and regarding *Arenaria ciliata* Lundager records "dense and

large tufts." But these forms are hardly typically pulvinate in habit.

Adventitious roots may be found in the interior of dense mesocorms.

Winter-stage. *Cerastium alpinum* appears to be particularly evergreen. HELGI JÓNSSON examined it in East Iceland on January 2nd; he mentions the dense hairy-covering of the protecting leaves (see Fig. 10). The living leaves contained starch. He found living leaves also on *C. caespitosum*, as SYLVÉN did in Central Sweden. Likewise, there evidently occur living leaves on *C. alpinum*, according to material preserved in alcohol, both at Upernivik on the west coast of Greenland (C. Ryder) and in N.E. Greenland (Lundager). But I found no starch in them. LUNDAGER and OSTENFELD (1917, p. 20) write about *C. alpinum* in N.E. Greenland: "When the flowering plant, in the autumn, is suddenly covered with snow, which remains during the winter, all the parts of it are so well preserved, that in the spring, when the snow has melted, they appear again and apparently are as fresh as if they had quite recently unfolded themselves."

The older branches, as in the other types, are apparently dead, because their bark is grey and wrinkled. This is most distinctly seen in the prostrate branches; but in the spring, fresh leaves develop from their terminal and lateral buds. It is true that the bark-layer is dead, but on loosening it, a fresh, green axis is found under it. In Denmark the same thing happens in nature. I have described and figured the wrinkled, older, subterranean runners which are also found in *Honckenya*. Perhaps this phenomenon should be regarded as a means of protecting the stem against transpiration due to cold winds.

E. The Cerastium arvense type.

This type differs from the preceding, by the fact that the prostrate shoots with elongated internodes, have not so short internodes at their base, that they may have there rosettes or rosette-like shoot-forms; also they develop roots so abundantly that they might justly be termed "creeping," and vegetative propagation (layering) must be able to take place both by means of aërial runners and — in some species — by subterranean runners. It is a further development of the *Cerastium alpinum* type.

To this I refer: *Cerastium trigynum*, *C. arvense*, *Moehringia lateriflora*, *Stellaria longipes*, *S. borealis* and *Honckenya peploides*. To these may be added of non-Arctic species, for instance *Stellaria graminea*, *S. nemorum* (Warming, 1918, Fig. 14), *S. holostea*, *S. uliginosa* and *S. glauca*, each with its special peculiarities.

When, under the *Cerastium alpinum* type, mention was made of pale, subterranean, plagiotropic shoots, they were probably aërial shoots which had been accidentally covered over with wind-carried soil and leaves, or had been developed in the shade. Those we are now discussing are, on the other hand, typical subterranean runners with elongated internodes, pale in colour, with scale-leaves and furnished with an apex which can push its way into the soil; but of course the boundary line between these two types is not sharp.

Cerastium trigynum we will first mention. It has, on the whole, the same mode of branching as *C. alpinum*, but the stems have their internodes, also those at the base, as a rule, elongated. Sylvén mentions, however, rosette-like shoots in the young plants in their first year, and Thekla Resvoll (loc. cit. p. 137, with Fig. 11) records that, in the snow-fields, the internodes of the primary shoot remain short even for a longer period. Branches, at any rate, are developed

most abundantly at the base, and therefore, numerous branches proceed from a central point, which is the upper end of the primary root. They may, in some cases — at any rate as long as they are still short — be more or less erect, with curved and rooting branches, but soon they lay themselves upon the ground, spreading out in all directions and rooting as aërial shoots, and in a comparatively short time they may attain a length of 10—25 cm, or even more. Ultimately many slender adventitious roots are thereby fastened to the ground, and by this means vegetative pro-

Fig. 11. *Cerastium trigynum.*
A runner (about $^1/_1$). As far as to L, reckoned from the flower, the foliage-leaves are fresh, then come dead foliage-leaves which subtend small shoots. Two leaves have been magnified. (Iceland; C. H. Ostenfeld). (E. W.)

pagation may take place (Fig. 11). The apices may be curved slightly upwards and the leaves may be unilaterally curved (Fig. 11). From these runners a few or several flowering shoots rise into the air; their duration of life is two years (Thekla Resvoll). Sometimes the shoots are so richly branched and so closely interwoven that broad, but low cushions may almost be formed.

Cerastium arvense has erect or ascending long-shoots, with short, sterile shoots at its base. It also develops plagiotropic shoots quickly, and the seedling may, under cultivation, develop, in the year of germination, a richly branched shoot-system, with typical scale-leaf-bearing runners. It may be densely branched at its base.

Stellaria longipes. The primary root lives for a long time. This species has prostrate shoots with very long internodes, with a few or several adventitious roots, and with very distinct, long and thin, scale-leaf-bearing runners, each with a straight apex.

Stellaria borealis. The stems are thin, spreading and often very long. From the basal nodes there proceed typically pale, very slender subterranean runners — shoots bearing scale-leaves.

Moehringia lateriflora has long, thin, prostrate and rooting shoots, with long internodes, and, as far as could be observed, thin subterranean runners, with slender roots proceeding from the leaf-axils.

Fig. 12. *Stellaria crassifolia.* Its winter-buds are densely filled with starch. (From Tromsø). (E. W.)

Honckenya peploides is the species which has the most decidedly typical, strong and far-spreading subterranean runners. The Arctic specimens appear to agree exactly with the Danish as regards the peculiarities of their runners, their serially-placed axillary buds, their dwarf-shoots with as many as 45 close-set leaf-pairs, etc. (described and figured by Warming in 1877—79, see also 1891, 1906, 1918, Fig. 12).

The germination is described by Joh. Erikson (1896). When growing on beaches, the cotyledons and the lowermost internodes of the epicotyl stem are buried in the sand by the wind, and are thereby, and perhaps also by root-contraction, carried down into the ground. In

each of the axils of the cotyledons, most frequently three serial buds are developed, the uppermost being the largest.

Pulvinate forms. In these species, in which the shoots with elongated internodes immediately become prostrate and spread out in all directions, the typical development of semi-globular cushions must be very difficult, if not impossible. In places where there is active growth, flat cake-shaped forms can however occur, being formed by the interwoven stems.

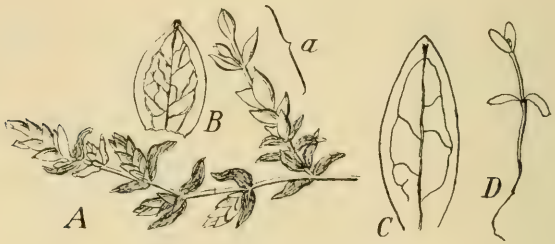

Fig. 13. *Stellaria humifusa.*
A, A branch with both dead and fresh leaves; *a*, a fresh-green portion. *B*, An old leaf, the veins are distinctly seen. (Upernivik).
C, *D*, a leaf magnified and a seedling. (Egedesminde; 28. 7. 1884.) (E.W.)

F. The Stellaria crassifolia type.

To this I refer *Stellaria crassifolia* and — with doubt — *S. humifusa.*

This type, which is represented by *S. crassifolia*, differs from the *Cerastium arvense*-type by developing small aërial (and? subterranean) hibernacula, organs which live through the winter and consist of short, thick-leaved shoots, rich in starch (Fig. 12). They are developed during the autumn (late summer), are liberated the next year, and then grow out into new plants by developing adventitious roots. Otherwise it resembles *Cerastium trigynum* in its mode of growth; the leaf-shoots with long internodes proceed from the same

root and lie prostrate along the ground, and are of a length of about 25 cm or perhaps even more; some are subterranean.

These hibernacula are described by Norman (1893) in his "Flora Arctica", p. 26 (Christiania Videnskabsselskab), and are figured by O. Nordstedt in 1909 (Bot. Notiser, p. 51).

The germination is described by Sylvén (p. 298). A seedling develops in the first year a plagiotropic, very richly branched aërial-shoot-system, of which some of the shoots often become subterranean by being covered with sand.

Stellaria humifusa should perhaps be most properly placed by the side of *Cerastium trigynum*. From the base of the primary stem proceed, as in *Cerastium trigynum*, numerous prostrate, richly branching and rooting, entangled branches. On these are found small, thick-leaved shoots, with short internodes, which are no doubt winter-shoots, and when the buds open in spring, they do not seem to elongate. In specimens collected on July 27th, far northwards (Upernivik), some of these shoots had unfolded and flowered, while others had not (see Fig. 13).

This species has a distinct, fairly long, but slender primary root. In addition to the creeping aërial shoots, subterranean shoots may occur.

With the exception of the above-mentioned short shoots, it is hardly to be called evergreen.

The shoots flower after a vegetative stage varying from two to several years.

G. The Stellaria media type.

The last growth-form is represented by the present species, which is widely distributed, but cannot be included among the truly Arctic species. It has, however, been found in several places in Greenland, north of the Arctic Circle,

and, according to Porsild, far from present and former settlements, and in other places for instance together with *Ranunculus hyperboreus.*

It is a hapaxanthic, summer-or winter-annual species, and does not appear to deviate from this rule in Arctic countries. The fullest account of it has been given by Wittrock (1908). According to him, in Central Sweden, the winter-annuals may begin to flower even during the autumn; they continue flowering in the milder period of the winter and bring it to a termination in the spring, with an abundant seed-production. There, the winter-annuals are the most vigorous, owing to the fact that numerous adventitious roots are developed during the autumn, on account of the increased dampness of the soil. Wittrock's figure shows that the adventitious roots proceed from the leaf-axils, and that they may branch freely. A very distinct account of these conditions is given by Korsmo (Fig. in his valuable work "Ugræsplancher"). If the branches have been detached from the parent-stems, in some way or other, vegetative propagation may thereby take place. In such a case it may perhaps also become pollacanthic, as an observation made by Bonnier also seems to indicate.

Other species also, in addition to being pollacanthic, are sometimes described as hapaxanthic, for instance *Sagina procumbens* and *Sagina Linnaei.* It is not improbable that this may be the case.

II. Leaf Anatomy.

With regard to the anatomical structure of the Arctic leaves the reader is more particularly referred to Bonnier and Börgesen, and in "Meddelelser om Grönland", vols. 36 and 37, to a series of treatises by Henning E. Petersen,

O. Gallöe, A. Mentz, Knud Jessen and Mathiesen. See also Th. Holm; Lazniewski may also be consulted.

The foliage-leaves are dorsiventral or almost isolateral (central).

The difference in the leaves is evidently connected with their breadth and the direction of their growth. In the broad-leaved species (the *Melandrium*-type) dorsiventrality prevails with palisade-tissue on the ventral side; see for instance

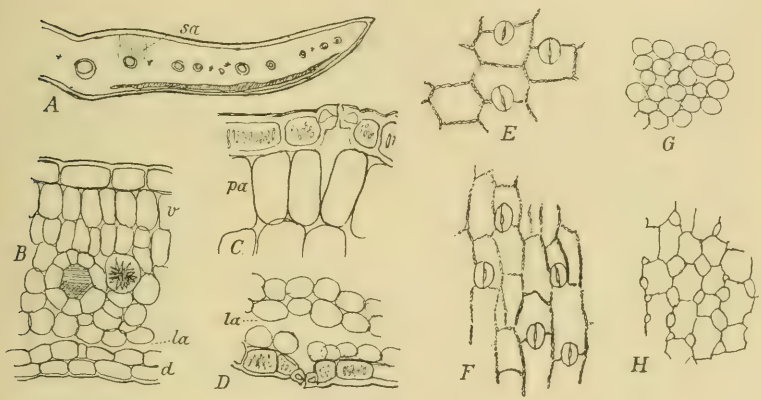

Fig. 14. *Viscaria alpina.*
(West Greenland; 24. 7. 1887; Lytzen.)
A, In the transverse section of the leaf is seen on the dorsal side a large lacuna, and on the ventral side a distinct palisade-tissue (*sa*); the crosses (xx) indicate cells with crystals of calcium oxalate; round the vascular bundles are sheaths. *B*, Transverse section of a leaf. *C* and *D*, Details from ventral and dorsal surfaces, more highly magnified. The epidermis of the ventral surface is distinctly higher than that of the dorsal surface; there are stomata on both surfaces. Pores are seen in the lateral walls of the epidermal cells. *E* and *F*, Epidermis of ventral and dorsal surfaces; the walls are highly porose. *G* and *H*, Section through the palisade-tissue and the spongy-tissue. (E. W.)

Viscaria alpina (Fig. 14 and the explanation of the figure); here the dorsiventrality is expressed by the fact that on the ventral side there are two layers of palisade-cells, while on the dorsal side there is a spongy-tissue of rounded cells, with

a large lacuna (*la* Fig. 14, *A*, *B* and *D*); then again in the height of the epidermis of both surfaces (*B*, *C* and *D*); in the form of the epidermal cells (*E* and *F*); in the form of the cells of the mesophyll (*G* and *H*); and lastly in the height of the cells which form the sheaths of the vascular bundles, since these cells are higher on the dorsal than on the ventral side (*B*).

Similar, but not quite so decided dorsiventrality is

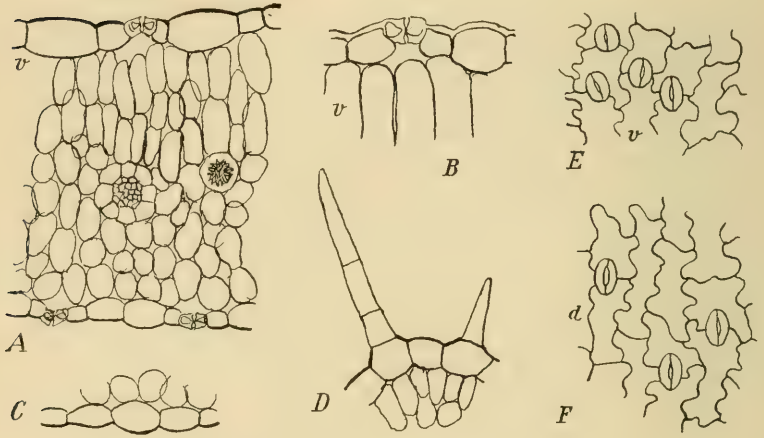

Fig. 15. *Melandrium involucratum.*
(From West Greenland; 30. 7. 1887; C. Ryder.)
A, Transverse section of leaf; the ventral side (*v*) has higher epidermis than has the dorsal side; compare the somewhat more highly magnified *B* and *C*. *D*, Hair. *E*, Epidermis of ventral surface and *F*, of dorsal surface. (E. W.)

found in *Melandrium involucratum* (Fig. 15, *A*, *B* and *C*, as also *E* and *F*).

Also in the much more narrow-leaved species *Silene acaulis* decided dorsiventrality is found; this is probably connected with the fact that the leaves are more or less horizontally placed (Fig. 3). Here also the dorsiventrality is expressed in the structure of the mesophyll (Fig. 16, *A*); in

the epidermis (it is devoid of stomata and is higher on the dorsal than on the ventral side: *A*, *G*, *H* and *J*; a few stomata, however, may occur towards the edge of the leaf), and in the sheath round the vascular bundles (*A* and *D*). For the rest, these features may vary somewhat, probably according to the prevailing conditions of the surroundings, but, on the whole, I found the structure of the leaves to be similar in plants from W. and E. Greenland, Iceland and Norway.

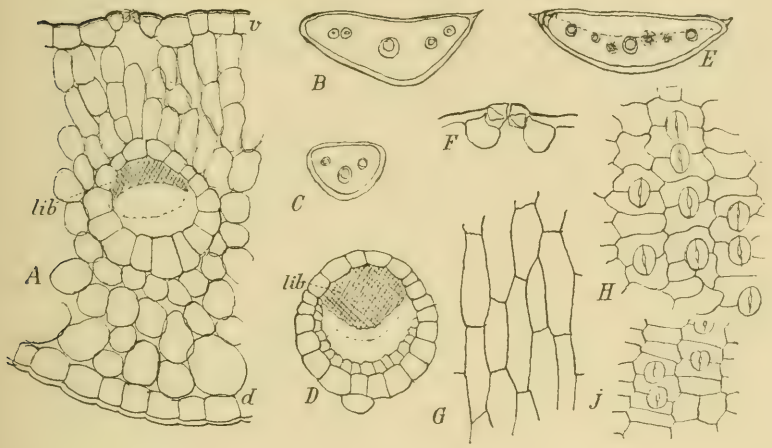

Fig. 16. *Silene acaulis.*
(From Iceland: *A*, *B*, *C*, *F*, *G* and *H*. From W. Greenland: *D* and *E*.) *A*, Transverse section of leaf; *lib*, bast; *d* is the dorsal surface, which has no stomata (see *G*) and is slightly higher than the ventral surface (*v*), which has numerous stomata (see *H*). The forms of the epidermal cells are seen in the same figures. *B* and *C*, Transverse sections of leaf. *D*, Transverse section of vascular bundle; *lib*, bast. *E*, Transverse section of leaf, four vascular bundles are seen and three cells with crystals of calcium oxalate. *F*, Stoma. *J*, Epidermis of ventral surface: the cell-walls are less undulating than in *H*. (E. W.)

That it depends on the direction of the leaves (their position with reference to the light) whether they become isolateral or dorsiventral, was also pointed out by me in 1891, in the case of the *Honckenya*; they are isolateral when directed upwards, and dorsiventral when horizontal.

The leaves of *Silene acaulis* are often somewhat oblique in transverse section (Fig. 16, *B*).

Cerastium alpinum also may have distinctly dorsiventral structure (Fig. 17); this is probably connected with the position of the fairly broad leaves which are found also in this species. The difference between the epidermis of the dorsal and the ventral surface is not so great as in the species already mentioned: there are stomata on both surfaces; but

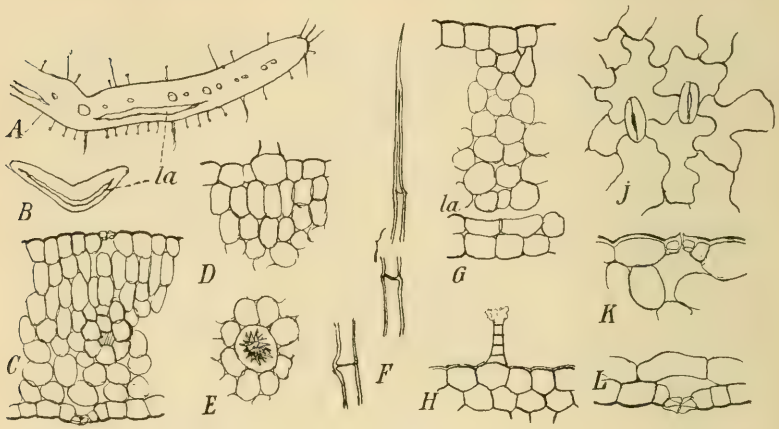

Fig. 17. *Cerastium alpinum.*
(From Greenland and Iceland.)
A, Transverse section of leaf, the two kinds of hair are indicated. There are two lacunæ (*la*). *B*, A similar section of a leaf from a bud. *C*, The transverse section shows that there are stomata on both surfaces, that palisade-cells are indicated in the thin-walled, lacunose mesophyll, and that there is a sheath around the vascular bundle. The epidermal cells are nearly of equal height on both surfaces, perhaps if anything, a little higher on the ventral surface. *D*, From ventral side. The base of a hair is seen. *E*, Cell with crystal of calcium oxalate. *F*, Three portions of one and the same hair. *G*, Transverse section of a leaf, recently cleared of snow; *la*, lacuna on the lower side. (Upernivik; 7. 5. 1887; C. Ryder.) *H*, A glandular hair (dorsal surface). *J*, Both leaf-surfaces have highly undulating epidermal cells and stomata. *K*, Epidermis and stoma of ventral surface. *L*, Same of dorsal surface. (E. W.)

the epidermis of the ventral surface is somewhat thicker than that of the dorsal (Fig. 17, *K* and *L*). Whether the

high degree of isolaterality shown in Fig. 17, *G* is due to the fact, that this leaf had recently been cleared of snow, or to some other cause, I cannot tell. The specimens from Iceland showed essentially the same structure as those from Greenland.

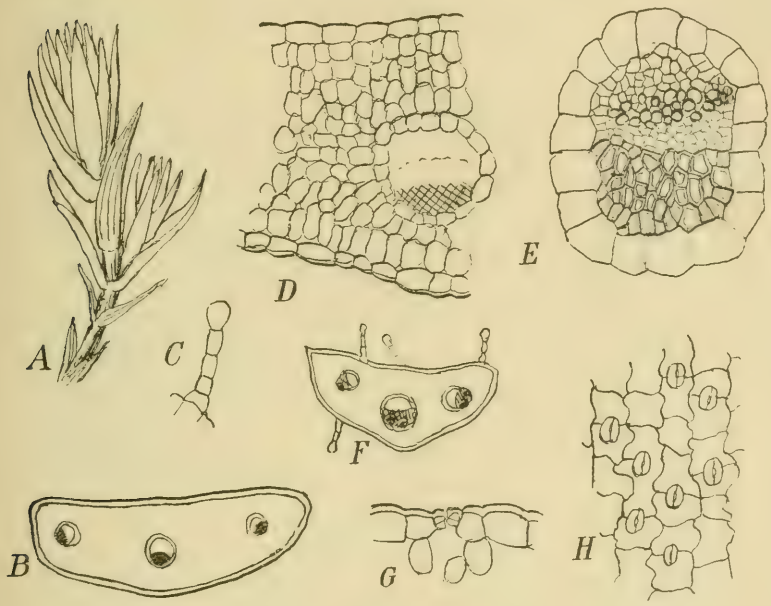

Fig. 18. *Minuartia verna.*
(From N.E. Greenland; 27. 6. 1908; A. Lundager.)
A, A small shoot with a branch. *B* and *F*, Transverse sections of leaf. There is strong bast tissue on the dorsal side of the vascular bundles. *C*, A glandular hair. *D*, Transverse section of leaf. The sheath of the vascular bundle is of the same thickness all round; see *E*, in which the bast tissue, sieve tissue and the tracheal tissue are shown. *G*, Epidermis with stoma. *H*, Epidermis of ventral surface. (E. W.)

In the *Minuartia verna* figured in Fig. 18, *D*, decided dorsiventrality also prevails, but here the palisade-tissue is on the dorsal side — probably in harmony with the erect position of the leaves (*A*).

In *Minuartia groenlandica* I found distinct palisade-tissue on the ventral side, but in the specimen investigated the leaves were, in contradistinction to those in *M. verna*, directed decidedly outwards. The epidermis of the dorsal surface was distinctly thicker than that of the ventral surface.

Stellaria humifusa (Fig. 19). According to the transverse sections shown in Fig. 19, *B* and *C*, this leaf is but slightly

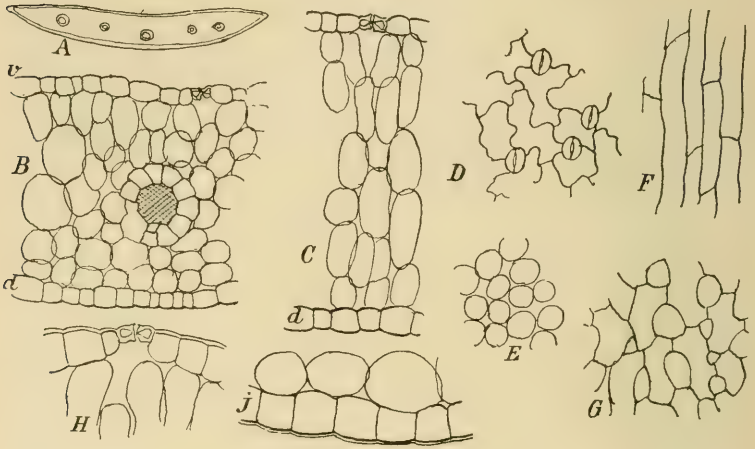

Fig. 19. *Stellaria humifusa.*
(From East Greenland; 15. 7. 1885; P. Eberlin.)
A, Transverse section of leaf. *B*, The same, more highly magnified; *v*, ventral surface; *d*, dorsal surface. *C*, A transverse section, the epidermal cells are nearly equal in height, which is seen more distinctly in the more highly magnified *H* (from the ventral surface) and *J* (from the dorsal surface). *D*, The epidermis of the ventral surface, and *E*, the underlying mesophyll-cells. *F*, The epidermis of the dorsal surface and *G* the underlying mesophyll. (E. W.)

dorsiventral, but a closer observation proves the dorsiventrality to be stronger. The epidermis of the dorsal surface is but little thicker than that of the ventral surface (Fig. 19, *J* and *H*), but the ventral surface has cells with decidedly undulating walls (*D*), and is rich in stomata, while the dorsal surface has elongated cells with straight sides (*F*).

Moreover, the mesophyll which lies under the epidermis differed on the two surfaces (*E* and *G*). In a specimen from S.E. Greenland there was almost homogeneous, but indistinct, palisade-tissue on both sides.

Similar weak dorsiventrality I found also in *Cerastium trigynum* (Fig. 20), and *Minuartia biflora*, which latter may however have decided isolaterality (Fig. 21, *K* and *B*), but

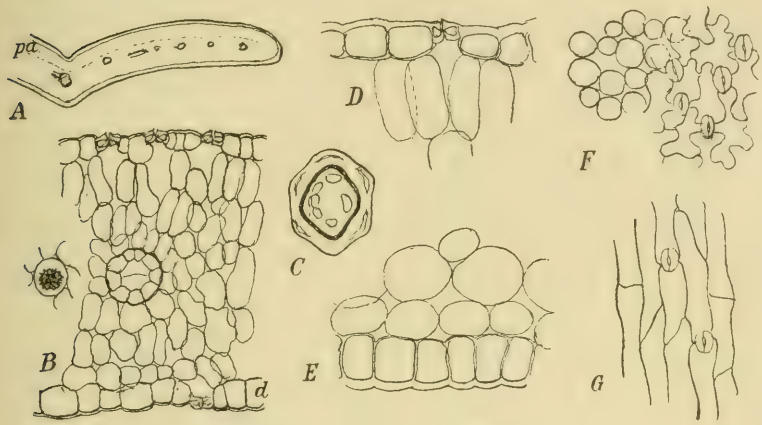

Fig. 20. *Cerastium trigynum.*
(From Iceland; C. H. Ostenfeld.)
A, Transverse section of leaf; *pa*, palisade-tissue. *B*, The transverse section shows the very lacunose structure of the thin-walled mesophyll; the epidermis of the dorsal surface (*d*) is higher than that of the ventral surface; there is a distinct sheath around the vascular bundle; there are about two layers of palisade-cells; *g*, a cell with crystal of calcium oxalate. *C*, Transverse section of stem. The black ring indicates the place of the mechanical tissue. There are five lacunæ in the cortex. *D*, From ventral side; epidermis and palisade-cells. *E*, From dorsal side. Magnification of *D* and *E* is the same, so that it is distinctly seen that the epidermis of the dorsal surface is thicker than that of the ventral surface. *F*, The epidermis of the ventral surface and transverse section of palisade-cells. *G*, The epidermis of the dorsal surface. (E. W.)

it differs in the epidermis of the two surfaces, which, as it however appears, cannot be connected with the fact that the leaves may be directed upwards, with the ventral surface

turned inwards, as in Fig. 21, *A*; they may also be directed straight out and curved backwards. More decided dorsiventrality with two layers of palisade-cells on the ventral side, was found in a specimen of *Cerastium trigynum* from Iceland.

Palisade-tissue on both sides I have moreover found

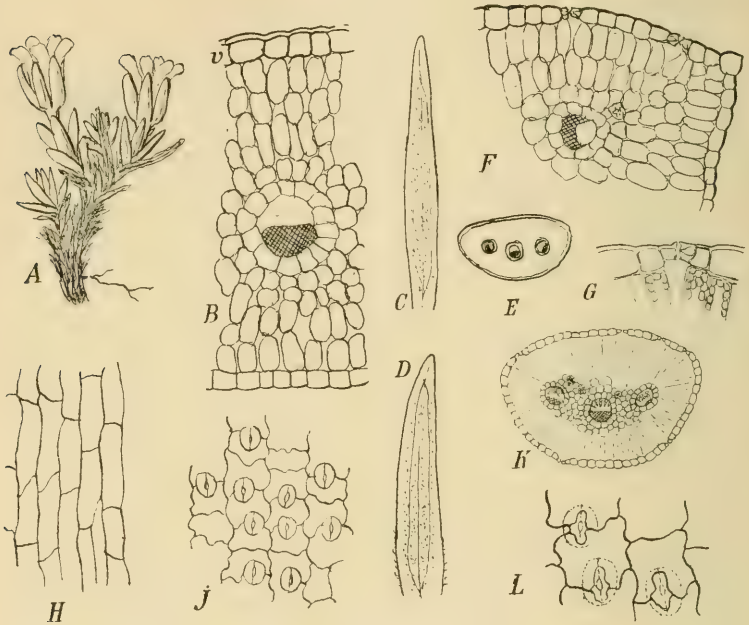

Fig. 21. *Minuartia biflora.*

A, From N.E. Greenland; 27. 6. 1908; A. Lundager. *B*, Transverse section of leaf; the cross-hatched part is the mechanical tissue; the two leaves, *C* and *D*, which belong to *B*, show the venation; the fine dots indicate cells with crystals of calcium oxalate. *E*, Transverse section of leaf. *F*, Margin of transverse section of a leaf; to this belongs the more highly magnified *G*. *H*, Epidermis of ventral surface. *J*, Epidermis of dorsal surface. *K*, Transverse section of leaf, centric structure. *L*, Epidermis of dorsal surface, seen from within, the outlines of the air-cavities under the stomata are distinctly seen.

From N.E. Greenland: *A*, *E*, *F*, *G*, *H*, *J* and L; from W. Greenland (Holsteinsborg; 4. 8. 1885; Rosenvinge): *B*, *C*, *D* and *K*. (E. W.)

in *Honckenya*; it was however highest on the ventral side. Stomata occur on both surfaces. According to Heinricher,

isolaterality is, for the rest, common in the *Caryophyllaceæ*, which must be connected with the fact that the leaves in many of the species are narrow, and can therefore be illuminated equally on all sides.

With regard to the mesophyll in general, the following may moreover be remarked. Vesque had already recorded in 1883 that the mesophyll in the *Caryophyllaceæ* consists of large cells, which are loosely connected so that it is rich is intercellular spaces, and "spongy" ("spongieux"). This is no doubt especially applicable to the Arctic species. This feature is not only found in the species figured above, but in as high a degree in *Cerastium nigrescens* and *Arenaria ciliata* (Figs. 22 and 23). In the latter figure it is even highly isolateral, with almost uniformly rounded cells. That it may be more compact is evident from what Th. Holm says regarding it.

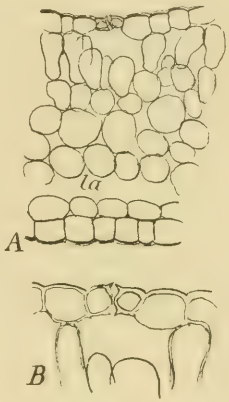

Fig. 22.
Cerastium nigrescens.
(From Dovre; 15th June; E. W.)
A, The transverse section of leaf shows a very lacunose tissue, with palisade-cells, and a lacuna (*la*) in the spongy-tissue. *B*, Stoma of ventral surface. (E. W.)

"It has already been emphasized by others (Bonnier and Börgesen) that it is a feature common to all the Arctic species, for the palisade-tissue to be most frequently imperfectly differentiated, the layers few in number, the height of the cells inconsiderable, and the intercellular spaces large — at any rate, not so strong and compact as in species from more southern — for instance Mediterranean — countries. Börgesen even found no palisade-tissue at all in specimens of *Silene acaulis* (l. c. Fig. 12) and *Minuartia verna* f. *hirta*; see also *Arenaria ciliata* in Th. Holm (Pl. XII, 2).

This is evidently a structure which is due to the faint light and the damp surroundings, and which contrasts strongly with the leaf-structure of the Alpine plants (Wagner and Börgesen).

In contradistinction to the Arctic *Caryophyllaceæ* we may refer e. g. to *Silene Otites* from dunes near Montpellier, which has palisade-tissue on both sides (Warming, Halofyt-studier, 1897, p. 203) and *Silene nicæensis* from Cadix (ibid.,

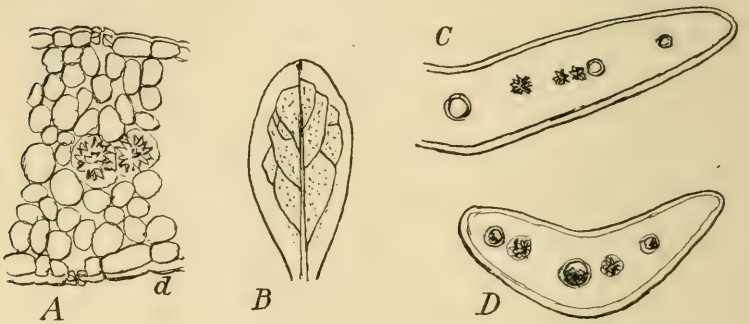

Fig. 23. *Arenaria ciliata.*
(From N. E. Greenland; 12. 7. 1908; A. Lundager.)
A, Transverse section of leaf; two cells with crystals of calcium oxalate. *B*, A leaf; the dots indicate cells with crystals. *C*, *D*, Transverse section of leaf, showing the crystals. (E. W.)

p. 198), together with *Honckenya* from Denmark which, when growing on sand strongly exposed to the sunlight, can have several layers of palisades on both sides (Warming, 1891, Fig. 12).

Many records as regards anatomical differences in plants from different countries, and variations in the same species from different habitats, and in different countries, are found in HEINRICHER, BÖRGESEN, WARMING and others. It is evident that the local conditions prevailing in the habitats, are in epharmony with the differences in the individuals. As an example of this, the reader is referred e. g. to JOH. SCHMIDT's

experimental investigations of *Lathyrus maritimus* (Bot. Tidsskrift, Köbenhavn, 1899, p. 22).

The different points of information concerning the leaf-anatomy of Alpine plants, may profitably be compared with those concerning that of the Arctic leaves. Schröder, in his excellent work "Das Pflanzenleben der Alpen", mentions the first-named and gives a resumé of Bonnier's and Wagner's results, which, in certain directions, show deviations from the Arctic species, especially as regards the palisade-tissue. When the Arctic plants have, on the whole, less differentiated palisade-tissue than the Alpine species, this must be especially attributed to the fainter light and the fogs in Arctic countries.

The fact that the mesophyll in Arctic plants is always thin-walled, and has abundant intercellular spaces, has been emphazied by previous authors, for instance Börgesen and Th. Holm; and is evident from numerous figures which a number of authors have published in the "Morphology and Biology of Arctic Plants", "Meddelelser om Grönland", Vols. 36 and 37 (for instance O. Gallöe, 1910; Knud Jessen, 1911 and 1913; Carsten Olsen, 1914; Mathiesen, 1916; H. E. Petersen, 1908, and others). In this, according to Wagner, there is a conformity with the Alpine species, a conformity which must be attributed to the greater moisture[1].

In *Cerastium arvense* (from willow copses in Kangardluarsuk in West Greenland) the spongy tissue was of an unusual character, consisting more or less of stellately branched cells, for which reason the lacunæ were particularly large. There was a distinct palisade-tissue with at least 3 cells in a vertical row. The epidermal cells had undulating walls and stomata on both surfaces.

[1] For purposes of comparison see the anatomy of woody plants in Warming (1887), H. E. Petfrsen (1908), and Mentz (1909).

A peculiar lacuna is found in the leaves of many of the species. It is caused by the sub-epidermal cell-layer of the dorsal surface separating, for a shorter or longer distance, from the mesophyll lying internal to these cell-layers. The cells bordering on the lacuna are rounded off inwardly towards it. I have already in 1884 pointed them out in *Silene acaulis*, *Arabis petræa*, *Dryas octopetala*, *Draba incana* and *Saxifraga oppositifolia*, and they are found figured by TH. HOLM in *Stellaria humifusa* (Pl. X, Figs. 2 and 8), *Salix reticulata* (Pl. XII, Fig. 12) and species of *Saxifraga* (Pl. X, Figs. 3 and 5). See also BÖRGESEN l. c. In HELGI JÓNSSON (1895, p. 291) we find the accompanying figure (Fig. 24), which shows a section through a bud of *Silene acaulis*. In the figures given above these lacunæ are shown in Fig. 14, *A* and *B* (*Viscaria alpina*); Fig. 17, *A*, *B* and *G* (*Cerastium alpinum*); Fig. 22 (*Cerastium nigrescens*). I have also observed them in *Dianthus superbus*. I cannot imagine that they are of any other use than as a protection against cold, since they must be bad heat-conductors.

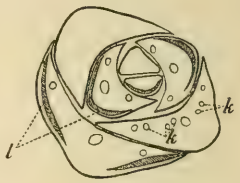

Fig. 24. *Silene acaulis*. (From Iceland; Helgi Jónsson.) Section through a bud. In each leaf three vascular bundles are seen; *k*, cells with crystals. On the dorsal side of the leaves air-containing lacunæ (*l*) are seen.

Crystals. With regard to the mesophyll, it may further be remarked, that in many species cells are found with crystals of calcium oxalate. They are situated in that layer of the leaves, in which the vascular strands are found, or at any rate, in close proximity to them. They are no doubt found in all the species. They are figured in Fig. 14, *A* and *B*; Fig. 15, *A*; Fig. 16, *E*; Fig. 17, *E*; Fig. 20, *B*; Fig. 23, *A*, *C* and *D*, and also in *B* where they are indicated by dots; their position is similarly indicated in Fig. 21, *C*

and *D*. I have seen them also in *Silene renosa*, *Honckenya* and *Minuartia hirta* (accompanying the three vascular bundles), and several authors mention them for instance Vesque (1883, pp. 130 and 133), Russel and Heinricher (see Pl. 30, *Silene inflata*). There may be a difference in individuals of the same species; in specimens of *Silene acaulis* from Finse in Norway there were many crystals of calcium oxalate, more than in the Icelandic individuals. Whether this difference be due to the season of the year, or to the habitat, I am not prepared to say.

Mechanical tissue I have not found except in certain cases, and then within the sheath around the vascular bundle mentioned below, for instance, on the ventral side in *Silene acaulis* (Fig. 16, *A* and *D*), on the dorsal side of them in *Minuartia verna* (Fig. 18, *B*, *D*, *E* and *F*), *M. groenlandica* and *M. biflora* (Fig. 21), and on both the ventral and the dorsal side, or only on the dorsal side (of the erect leaves) of *Melandrium involucratum* (from Upernivik). Records of this are also to be found in Börgesen, Vesque, and others.

The epidermis always consists of one layer only, and the cell-walls are rather thin on all sides, but are naturally thickest on the outer side. The cuticle is thin. This must be an adaptation to the nature of the habitat, and can vary with it. W. Russel has demonstrated, that the leaves of *Dianthus prolifer* have much thicker epidermal walls in the Mediterranean countries, than near Paris, and therefore become much stiffer.

Only in *Viscaria alpina* did I find the walls of the epidermal cells to be somewhat thicker, and the lateral walls porose (Fig. 14, *C*, *D*, *E* and *F*). The outer walls of the epidermis were found to be thick in *Sagina nodosa* from dunes in Denmark.

That the dorsiventrality can be displayed in the various degrees of thickness of the epidermal cells of the ventral and dorsal surfaces, has been stated above. It appears, as already mentioned, to be correlated, with the direction of the leaves (the epidermis of the surface which is turned upwards or outwards being the highest).

The epidermal cells are arranged more or less regularly in longitudinal rows, at any rate in the narrow or linear leaves (see e. g. Fig. 14, *E* and *F*; Fig. 15, *E* and *F*; Fig. 16, *G*, *H* and *J*; Fig. 18, *H*; Fig. 19, *D* and *F*; Fig. 20, *G*; and Fig. 21, *H*, *J* and *L*).

The lateral walls of the cells, when seen from above, are sometimes highly undulating on both leaf-surfaces, although more highly on that surface which limits the spongy-tissue than on the other surface (Fig. 15, *E* and *F*); more frequently the epidermal cells of the one surface have undulating lateral walls, while those of the other have only slightly undulating or quite straight walls; as also the cells of this surface are more elongated (Fig. 14, *E* and *F*; Fig. 16, *G*, *H* and *J*; Fig. 19, *D* and *F*; Fig. 20, *F* and *G*; Fig. 21, *H*, *J* and *L*). The cells with very highly undulating walls are moreover very short. The undulations indicate more damp or more shady conditions.

The Stomata are lower than the other epidermal cells, and are placed on a level with the outer surface of the epidermis, or even project slightly above it (this is shown in many figures). Stomata may occur on both surfaces, sometimes almost equally in number. In other cases, the one surface has no stomata or only a few. In some cases they are most numerous on the dorsal surface, in others on the ventral surface, for instance in *Stellaria humifusa*. All these circumstances have been fully treated of by VESQUE, BÖRGESEN, WAGNER and BONNIER (see also TH. HOLM). As

regards the number of stomata per unit of surface the reader may be referred, for instance, to Børgesen.

The apertures of the stomata, at all events in the narrow-leaved species, lie parallel with the longitudinal axis of the leaf.

That the guard-cells are surrounded by the other epidermal cells in a peculiar manner, was, as far as I know, first pointed out and figured by Vesque (Anm. sc. nat., 1883, 6. Sér., 15, p. 130): "Les stomates sont embrassés par deux cellules dont la cloison separatrice et perpendiculaire à l'ostiole". See the preceding Fig. 14, *E* and *F*; 15, *E* and *F*; 16, *H* and *J*; 17, *J*; 19, *D*; 20, *F*; and Fig. 21, *J* and *L*, all of which, in addition, show, here and there, a small deviation of minor importance, in that an aperture may be surrounded by 3—4 cells, but each end of the stoma is always limited by a more or less crescent-shaped cell.

Hairs are found in many of the species, in some even in such great numbers, that they become quite pilose, this is especially the case in *Cerastium alpinum*, which is otherwise exceedingly variable as regards the extent to which it is hairy. The hairs are of two kinds, both consisting of a single row of cells arising from a single epidermal cell, as already pointed out by Vesque (1883). The one kind of hair is thick-walled and dead (filled with air), and terminate in a point (Fig. 15, *D* and Fig. 17, *F*); they are specially numerous in the form *lanata* of *Cerastium alpinum*. Their function must be to protect the plant against excessive transpiration. The other kind of hair is secretory, and its terminal cell is globular (see for instance *Minuartia verna*, Fig. 18, *C*, and *Cerastium alpinum*, Fig. 17, *H* and *A*).

The Vascular bundles. It is, at all events in the narrow-leaved species, only a single bundle, which from the stem enters into the leaf, and there quickly develops a

branch on each side, which may itself branch ogain (Fig. 21, *C*, *D* and Fig. 23, *B*). In the most narrow-leaved species this does not often happen, so that the entire number of bundles in a transverse-section will be three only (Figs. 18 and 21) — these are especially prominent in older leaves which have been emptied of their cell-contents, — but more frequently there are several, or even many, in the broadest-leaved specimens (Figs. 14, 17 and 20). As regards the vascular tissue, I have no particulars to communicate.

In some of the species mechanical tissue occurs on the ventral or dorsal side of the strongest vascular bundles, as mentioned above.

It appears to be an exceedingly constant characteristic in the *Caryophyllaceæ* to have around the vascular bundles a thin-walled, sharply differentiated sheath consisting of one layer of cells, which are almost square in transverse section; this is illustrated in most of the figures given above. In the majority of cases, the cells are of equal height, but cases may occur in which those of the dorsal surface are higher than those of the ventral (e. g. *Silene acaulis*, Fig. 16, *A*, *D*).

For further particulars regarding the anatomy of the *Caryophyllaceæ*, the reader is referred for instance to Regnault (1860; Ann. sc. nat., 4. Sér., 14); Seignette (Revue gen. I, p. 564); O. G. Petersen (Botan. Tidsskr., København, 1888); Heinricher (1884); Joh. Erikson (1896); Warming (1890, 1891, 1897) and Solereder. As regards the structure of the leaves in the Alps, see Wagner, Laźniewski and C. Schröeter.

III. Adaptions to the Environment.

The morphological and anatomical structure of plants is, in the first place, dependent upon their genetic relation-

ships, but it will be difficult or rather impossible to demonstrate the origin or utility of their genetic peculiarities (for instance, why the leaves in the *Caryophyllaceæ* are opposite; the origin of the peculiar manner of branching with only one shoot, or at all events only one vigorous shoot, from each pair of leaves, and of the position of these shoots in a peculiar spiral; or the origin of the one-layered sheath, around the vascular bundle, just mentioned). As regards the *Caryophyllaceæ* Vesque (1883, p. 133) has rightly stated that "La famille des Caryophyllées est des plus naturelles et des mieux limitées". This is true both as regards the morphological and the anatomical structure and, as far as I can see, cannot be explained ecologically. Also as regards the structure of the flowers, there are very great similiarities in the different genera.

In the second place, the peculiarities of plants are dependent upon the ecological factors of the habitat, i. e. the climatic and edaphic conditions which prevail there. It is consequently of importance that we should be accurately informed with regard to these points, but the truth is, we have information only about the general features of the climate and — possibly — of the soil. As regards the conditions which prevail in the special, local habitats in which the different individuals have been gathered we are, so to speak, never told anything. Unfortunately, there are many travelling botanists who find it sufficient to state, that such and such species have been found here and there, and to record the geographical situation; but as regards the conditions found to be prevailing in the habitats in question, they tell us nothing whatever. This is however a great drawback, for without doubt the ecological factors, or the differences which prevail in the habitats, are exactly that which sets a different stamp upon individuals of the same species.

Of the botanists who have given the fullest information with respect to the natural conditions prevailing in the habitats in Greenland, I must, as regards the *Caryophyllaceæ*, point out most particularly JENS VAHL (in the Arctic Herbarium belonging to the University of Copenhagen) and CHR. KRUUSE (in his papers on the plant-growth on the east coast of Greenland in "Meddelelser om Grönland" Vols. 30 and 49). To mention the numerous data to hand, would take us too far; here it must suffice to refer to the Floras and especially to JOH. LANGE's "Conspectus"; I therefore give the following short resumé.

With regard to the climate of the habitat, we know, in a general way, for instance, that it becomes drier the farther we proceed from the south up towards the north in Greenland, and from the coast towards the interior. See for instance the small map (after W. KREBS) reproduced in GUNNAR ANDERSON (1900). But the rainfall is hardly of as much importance as is the water accessible to the plants ecpecially from the ground and the fogs.

The soil is usually rather damp. One hardly goes too far if one asserts that a great moisture of the soil is an essential characteristic of Arctic nature. This is evident from the many descriptions, for instance in VAHL ("in locis humidis", "in locis humidiusculis", "in locis turfosis", "in locis uliginosis", "in pratis", etc.), or the frequent occurrence, in KRUUSE, PORSILD, LUNDAGER, and others, of expressions such as "on moist, barren ground", "on wet sand", "by preference in humid places", "near lakes or running water", "on sheltered, humid slope", "on moist rocky flats", "low-lying humid soil", "on damp, manured places", etc. JOH. LANGE has, as a rule, given tolerably clear information in his "Conspectus" about the nature of the soil, and his statements are presumably based upon JENS VAHL's labels.

His statements also verify the opinion that the majority of the species grow upon tolerably damp ground, many of them even upon wet or boggy ground.

The cause of the general dampness of the ground, is apparent. It is, in the first place, the snow-covering, during the long winter, which lies over the whole country, so to speak, and which only disappears for a few summer-months, and then from a part of the coast-land only. The melting snow soaks into the soil and trickles down over the sloping ground, for a long time especially in those parts where the rays of the sun can only reach it with difficulty, for instance, on slopes facing the north. Different travellers have drawn attention to the fact that the northern sides of mountains or those sides of valleys facing the north, remain fresh and green much longer than those facing the south.

From the Alps we hear much about "die Schneethälchen" and their peculiar flora (for instance Schröter, Brockmann-Jerosch and other Swiss botanists); also from Scandinavia (for instance Th. Resvoll). These isolated snow-patches which lie long, many during the whole summer, retain a considerable amount of moisture for a long time, and may be prolonged sources of water which will trickle down over the land. Even if plants grow upon a sandy substratum, or even upon a rocky substratum, this will long be able to remain wet or damp. A stony or gravelly substratum also retains moisture for a long time, because the ground is protected from evaporation by the covering or imbedded stones.

Even if travellers record, with regard to an individual plant, that it has been found on "dry ground," one must not take for granted that the ground has not been damp — even very damp. With regard to those plants, which have possibly been recorded to have been gathered "on manured

spots," we may also suppose with tolerable certainty, that the ground on which they grew contained much water. Some of the species, however, are not very particular in their demands, since they are recorded as growing in "all localities," or "everywhere," as for instance, *Cerastium alpinum* and *Silene acaulis*. The many varieties of the former perhaps stand in direct causal connection with small differences in the habitats.

Transpiration. A factor which is connected with what has been said above, and is of no less importance, is the extent of the transpiration and of the atmospheric humidity.

Th. Wulff stated (1912, p. 5) that "the Arctic Flora is of a decidedly xerophilous type." There are, it is true, decidedly xerophilous types in the Arctic vegetation, which I have probably been the first to record (1887) since I, in chapter 5 (pp. 105—127), treated of "The Adaptations of Heath-plants to Drought". It must, however, be remarked that the woody plants of the heath and the rocky-flat are what I especially treated, and amongst these one finds in reality a number of distinctly xerophilous types. I pointed out five different types of leaves, and even declared that similar types are met with in the steppes and in deserts — even in the Egyptian-Arabian desert, but I laid a great stress upon the fact that this essentially applied only to the woody plants of the heath.

By far the greater majority of the species in question are evergreens, this especially applies to the many woody plants proper, the foliage-leaves of which remain for more than one year. With regard to these one can speak of physiological dryness, but hardly with regard to low-growing herbs.

It is easy to understand that in woody plants the shoots must become xerophytic in structure, — which is, as usual,

exhibited in the anatomical structure of the leaves, — because they are higher in growth than are herbs, and often may be without a snow-covering during the winter; their leaves will frequently be exposed to the desiccating power of cold and dry wind and this in a higher degree than those of herbs, and the cold soil will for a long time prevent the roots from absorbing water. The winter, in particular, is a very dry season of the year, and the higher the latitude, the drier it becomes; but the danger of desiccation is much less as regards the vegetative organs of herbs, because they are generally lower in growth, and are, in addition, often protected by the dwarf shrubs.

If we now regard the leaves of the *Caryophyllaceæ*, we find no such adaptation for withstanding desiccation. On the contrary, in the structure of their leaves they remind one more of those of aquatic plants, or of herbs which grow on damp, shady ground in woods.

The epidermis has no specially thickened and cuticularised outer walls. The stomata are situated very superficially, occur often on both surfaces, and in great abundance; the epidermal cells are most frequently highly undulating; the mesophyll is very lacunose; aqueous tissue does not occur; the epidermis is on the whole glabrous, and in *Cerastium alpinum* alone a denser covering of hairs is found; and hard bast occurs rarely and only in a few thicker vascular bundles. These results agree, as already mentioned, with those previously arrived at by several botanists, as regards Arctic plants in general.

The explanation is obvious: The rays of the sun are very oblique; the leaves are but slightly warmed, although the insolation may be very strong locally; the atmospheric humidity is great (80—85 %; see table in Börgesen); fogs and cloud-covered sky are very frequent, also during

the summer; it is advantageous that transpiration is not lessened by special structural features, so that the water-current can flow rapidly through the leaves and the assimilation increase in vigour and compensate for the briefness of the summer, with its fogs and weak light. The transpiration cannot be assumed to be specially strong during summer. It is also easily compensated for by the water which is accessible to the herbs from the fogs and from the water-contents of the soil.

The precipitation undoubtedly varies greatly in the different regions. Lundager records from Danmarks Havn in N.E. Greenland 28.4 mm for the summer (April—Sept.) and 117.2 mm for the winter. Only $^1/_{10}$ falls as rain. The inconsiderable amount of rainfall must undoubtedly be compensated for by the water-contents of the soil and the fogs.

Thorild Wulff has, in his paper of 1902, communicated some results of transpiration-experiments with Arctic plants made with the cobalt-test in the open in Spitzbergen, detached leaves being placed between cobalt-paper. Wulff particularly emphasizes the fact that the method is defective, but no other could be employed. The water from the snow of the habitat situated on a high level "provided for a homogeneous distribution of the moisture of the soil." Unfortunately, he did not investigate the temperature of the water and the soil, which of course plays an essential part as regards the amount of the transpiration. Among the ten species which were investigated, there was only one of *Caryophyllaceæ*, viz. *Cerastium alpinum*, the leaves of which were woolly with dense hairs. The transpiration was exceedingly slight, which Wulff thinks was essentially due to the hairy covering, "as the anatomy of the leaf rather favours the belief in an excessive transpiration than tells against it." Among the plants used for the experiment, *Cerastium alpi-*

num belonged to those which had the least transpiration, and the slightest growth. The result does not appear to have been very conclusive, but he says that, on the whole, the Arctic plants which were investigated had only slight transpiration, compared with plants from more southern regions. This must, beyond doubt, be due to the atmospheric humidity, which is certainly greater during the vegetative period than outside it. The leaf-structure of herbaceous plants agrees well with the humid air, the fogs and the abundant water-contents of the soil. As regards the physiological dryness in Arctic countries certainly too much has been said. Thorild Wulff generalized in too high a degree in saying, that the Arctic flora "is of a decidedly xerophytic type," although this is true only of the woody plants.

The above-mentioned conditions pertaining to the habitat also explain, at any rate some of the morphological conditions, e. g., that in so many cases adventitious roots are developed; that runners are formed may be due to the fact, that the low temperature has altered the growth-direction of the shoots (Psychrokliny: Vöchting, 1898; Lidforss, 1903), the moisture, perhaps in connection with the pressure of the snow, having favorised a development of adventitious roots. On the other hand, it must be the cold and desiccating winds which cause the frequently-occurring pulvinate growth; the shoots are arrested in their growth, and the branches become short and thick-set.

That the buds are open and that bud-scales are absent, I regard as a generic character. This results in conditions favourable to the development of the pulvinate habit, especially when the plants are covered with a layer of snow, which lasts throughout the winter; many leaves must be able to keep green for a long time, at all events until the snow has melted, and the youngest leaves are ready for

quick expansive. In all Arctic *Caryophyllaceæ* it will certainly be found that the youngest leaves are, during the winter, protected by older leaves, which are more or less withered. That the peculiar condition of the protoplasm, and the different substances contained in the cells, can protect against the cold of the various seasons, must be taken for granted. With regard to this, however, I cannot give any new information.

IV. Flower-biology and Notes on Seed-production.

In by far the greater majority of the Arctic-flowering plants it appears that the flowers are formed during the year previous to that in which they open, and that they pass the winter in a more or less well-developed condition, — a circumstance which is a natural adaptation to the extreme brevity of the favourable season of the year (the extreme brevity of the summer-time).

In the foregoing papers in "Meddelelser om Grönland" belonging to this series, the fact that the flowers are formed during the year previous to that in which they open, has been specially pointed out in a number of species by KNUD JESSEN (Ranunculaceæ, Rosaceæ) and others, and for instance, as regards the *Caryophyllaceæ*, this is found to be the case in *Cerastium alpinum* in Iceland and the Færöes (Helgi Jónsson), *Silene acaulis* (*idem*), *Cerastium trigynum* in Norway (Th. Resvoll), *Melandrium apetalum* (*eadem*), and *Minuartia biflora*. On Greenland material, gathered on Aug. 6th, I found buds which enclosed flowers for the next year.

As an example I give here (Figs. 25) some figs. of *Silene acaulis*. The material was gathered by C. RYDER near Upernivik on ground which had recently been bared of snow. The buds which were present had evidently passed through the winter. The buds were $^1/_2$ mm in transverse section;

they were doubtless male flowers, all the leaf-whorls of which were formed, also that of the pistil (Fig. 25, the small figure to the left). For further particulars, see explanation of the figure. On material from South Greenland, gathered on Aug. 29th, I also found buds which enclosed flowers for the next year. That flowers buried in the snow, on the melting of the latter in the ensuing year, sometimes emerge "as fresh to look at as newly expanded", is evident from what e. g. LUNDAGER writes (1912) about *Cerastium alpinum* found in N. E. Greenland, May 23rd, 1908 (loc. cit. p. 409).

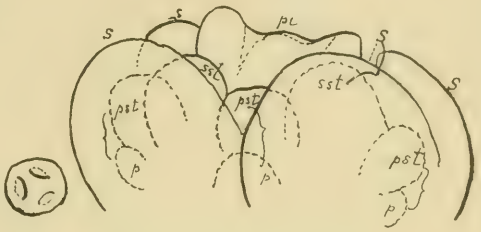

Fig. 25. *Silene acaulis.* Young bud, highly magnified and made transparent, so that through the sepals (*s*—*s*), drawn with continuous lines, the calyx-stamens (*sst*), the petals (*p*) and the stamens (*pst*) placed opposite to them are seen. The pistil is in the middle; it is at the stage of development shown in the small figure. From Upernivik, 10. 5. 1887; C. Ryder. (E. W.)

In "Botanisk Forenings Festskrift" (Copenhagen, 1890), I published a series of notes on the flower-biology of the Arctic and Danish *Caryophyllaceæ*, accompanied by 29 figures. These notes, which were written in Danish, without any Resumé in a universally current European language, appear to me to have remained almost unknown. I have, therefore, no hesitation in reprinting here such parts of them as concern Arctic species. My notes are based, for the most part, on observations made in the field in northern countries, and afterwards supplemented by studies made on material preserved in alcohol.

I had been hoping to find some contribution towards the elucidation of the nature of gynodioecism, but this

hope was not realised. It is to be hoped that others may be more fortunate in this respect, especially through experiments they may make.

I begin with the *Alsineæ* because I regard them as the most original type of *Caryophyllaceæ*: since their flowers are open and have polysepalous calyx and polypetalous corolla which are for the most part complete in number in all the whorls; can be visited by many kinds of insects; have many ovules in the ovary; and are hypogynous. From this prototype there issue on the one side the *Sileneæ*, the flowers of which have gamosepalous calyx and are in a higher degree adapted to pollination by special insects; and on the other side, the *Scleranthеæ*, with more or less reduced flowers.

1. Cerastium arvense. L.

Denmark. Gynodioecism; protandry. As the plant is propagated by underground runners, large patches are found covered with the one form only. The stigmatic papillæ extend almost to the base of the styles.

☿ are distinctly >[1] ♀, 13—15 mm in diam., petals 10—11 mm long, while ♀ are 10—12 mm in diam., petals 7—8 mm long. Highly protandrous with the ordinary process of development; the cal.-anth. are the first to open, the cal.-st. standing erect, then the cor.-anth., before the cal.-anth. are emptied, and the cal.-st. bend backwards; ultimately, the styles bend outwards, and the stigmatic papillæ grow out, as a rule before the pollen has fallen out entirely. Self-pollination may be able to take place. The anthers are usually

[1] For brevety's sake the mathematical signs indicating relations of quantities are used. For the same reason the following abbreviations have been used: cal.-anth. for anthers opposite the sepals, cal.-st. for stamens opposite the sepals, cor.-st. for stamens opposite the petals, etc.

placed transversely to the filaments, with the pollen lying exposed on the side turned upwards (Fig. 26, a^1) or even entirely outwards.

In Germany, according to A. Schultz, ♀ are not rare and are often the only form to occur over entire tracts. I do not know how frequent it is in Denmark. The anthers are generally distinct and almost normal in form, but they are white, transparent and empty. Sometimes a few (I have seen 1—3) anthers are met with among the others which are yellowish, dehiscent, and contain pollen-grains; the latter appear, however, to be useless, only a few being round and smooth, while the majority vary in size, are angular and thick-walled, and are therefore distinctly abnormal. It is also usual for such flowers to be somewhat larger (petals 9—10 mm) than those which are more decidedly female. In the neighbourhood of Copenhagen there is a growth of *Cerastium arvense* in which the flowers vary between ☿ and ♀ and there fruit is sometimes set, but, as far as I have observed, rarely.

Greenland (about 67° N. lat.). ☿. Protandrous. Petals 8 mm, cal.-st. 5 and cor.-st. $4^1/_2$ mm. Ovary 2 mm. Consequently, somewhat small-flowered, but otherwise normal.

2. Cerastium alpinum L. (Fig. 26).

Almost as large-flowered as *C. arvense*, but has nevertheless a decidedly homogamous and self-pollinating flower, which fact must undoubtedly be correlated with its northern (Arctic) and its Alpine homes. In Greenland I observed that the flowers after a two-days rain were somewhat more drooping, and more closed than usual.

West Greenland (as far as about 73° N. lat.). Gynodioecism; Gynomonoecism. — ☿. Slight protandry with

quickly ensuing homogamy and self-pollination (Fig. 26a, b^1). The relative length and position of the stamens and pistil is shown in the figures. Before the cor.-anth. are opened the styles may be covered with germinating pollen. I have even seen homogamy set in immediately, even before the flowers had expanded fully, and while the styles were still

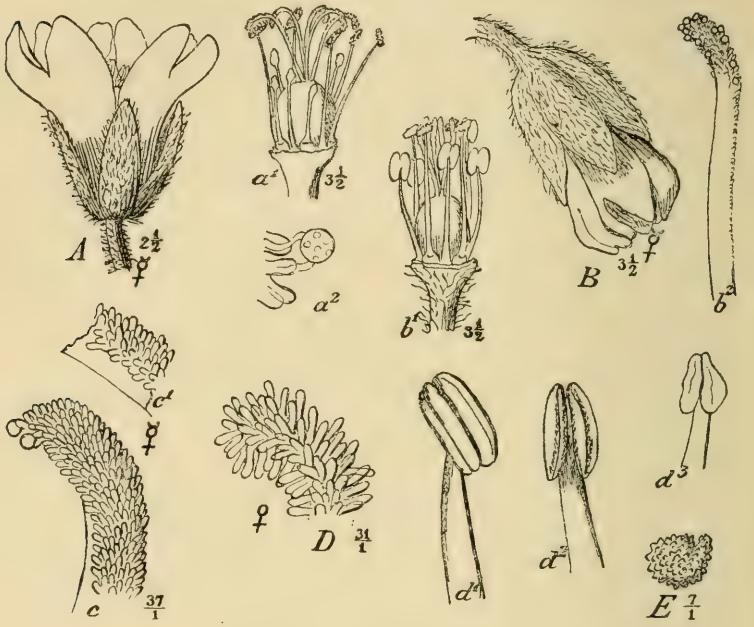

Fig. 26a. *Cerastium alpinum.*
From West Greenland (about 64°—70° N. lat.).
☿. — *A*, a^1, a^2: ☿ in which four cal.-st. and one cor.-st. are abortive (a^1). *B*: ☿, scarcely expanded, but the stigmas (b^2) are covered with germinating pollen; three cal.-anth. have opened, but the cor.-anth. (b^1) are still closed. *C*, Style of ☿ with pollen which has germinated; all the anthers have opened and are empty. c^1 shows the longest papillæ at this stage. — ♀. *D*, Style, $^{37}/_1$ and not $^{31}/_1$ (from beyond 73° N. lat.; C. Ryder), and d^1, d^2, d^3 stamens in various stages of reduction; d^1 has fibrous cells in the wall, but no pollen. *E*, Seed. (E. W.)

erect: in Fig. 1, *B*, b^1, b^2 the stigma is covered with germinating pollen although seven anthers are still closed. This

is almost self-pollination in the bud. In specimens from Upernivik (C. Ryder) the flowers were closed and the styles were closely surrounded by the anthers. — ♀ are very common in Greenland, as far as 73° N. lat. They are < ☿, the petals being 8 (to 10) mm in length (sometimes only slightly longer than the calyx), while in ☿ they are 11—12 mm long; the pistils appear to be the same, but the stigmatic papillæ are larger in ♀ (Fig. 26a, *D*) than in ☿ (Fig. *C*, c^1). The stamens may be abortive in varying degrees; the anthers may have a somewhat normal form, but be quite transparent, or the stamens might be, for instance, 4—4½ mm long and have yellowish anthers, which is, however, devoid of pollen (Fig. d^1—d^3). Near Godhavn I found one ♀ in the same tuft as ☿, consequently gynomonoecism. In several female flowers from Godhavn (69° N. lat.) I saw the stigmas densely covered with pollen-grains, so that insect-pollination must be able to take place.

Intermediate forms also occur, for instance, flowers with two normal stamens and the others sterile; or four cal.-st. and one cor.-st. abortive, or even eight normal and two quite abortive.

East Greenland. ☿ (gathered by P. Eberlin), agree with those from the west coast, but the flowers are smaller (petals 9 mm).

Fruit ripens in Greenland from the southern point up to at least Upernivik (seed, Fig. 26a, *E*).

Spitzbergen. ☿ (gathered by Nathorst; 1. 7. 1882), agree with those from Greenland. Fruit set, which ripens both here and I think in all other Arctic regions, e. g. Grinnel Land, Sabine Island, the north coast of Siberia, etc.

Var. β *cæspitosum* (Malmgr.), Fig. 26b, gathered by Nathorst. The specimens are very small (foliage-leaves 5 mm long and 3½ mm broad), quite glabrous; appear to have

foliage-leaves which persist through the winter, and not to differ from the type in regard to the flowers.

Iceland. (Reykjavik). Protandry.

Norway. As in Greenland, sometimes even protogynous (Alten, about 70° N. lat.; Tromsö). Gynodioecism: Kongsvold (16. 7. 87).

LINDMAN is of opinion that the anthers are placed so far above the stigmas that self-pollination cannot take place until in the last stage, when the fully grown and revolute styles may reach the anthers. — Sweden: Slight protandry (Axell). — The Alps: Gynodioecism; protandrous (but ♀ much rarer than ☿: Ludwig). — Italy: Homogamy (Ricca).

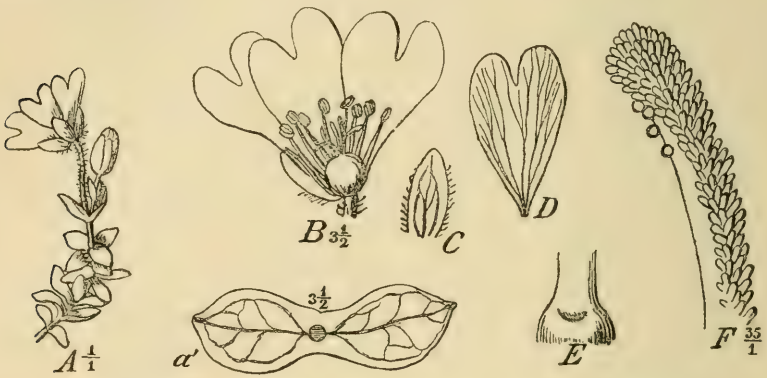

Fig. 26b. *Cerastium alpinum* β *cæspitosum* Malmgr.
From Spitzbergen (Nathorst; 20. 8. 1882).
A, A branch, natural size; lower part quite glabrous and with very small, close-set foliage-leaves; upper part covered with long, scattered hairs (not glandular hairs). The lowermost leaves have persisted through the winter. a^1, A pair of foliage leaves. *B*, A flower opened and its parts spread out artificially. *C*, Sepal. *D*, Petal. *E*, The basal part of a cal.-st. *F*, Style with germinating pollen-grains. There was still some pollen left in the anthers of the flower of which the style is shown in Fig. *F*. (E. W.)

3. Cerastium latifolium. L.

Norway (Dovre; 15. 7. 1887). ☿ have petals about 8 mm in length; the stigmatic papillæ extend downwards only $^3/_4$ or $^4/_5$ the length of the style. Slight protandry, but homogamy soon ensues, and in the specimens investigated

the styles were bending backwards so decidedly that they almost touched the petals and were more-or-less dipping into the pollen, so that self-pollination took place.

In one flower the styles were only slightly curved backwards, but were already covered with germinating pollen; of the anthers, only the cal.-anth. were open and had shed a little pollen. Here, consequently, a slight degree of protogyny, if anything, appears to have taken place.

Switzerland: Protandry, with ultimate self-pollination (H.M.).

4. **Cerastium trigynum** Vill. (Fig. 27).

(= *Stellaria cerastoides* L.)

Greenland: Gynodioecism with decidedly homogamous or slightly protandrous or slightly protogynous flowers. ☿ but rarely ♀; gynomonoecism rare. Self-pollination.

☿. The petals are only slightly outspread (Fig. 27, *A*) so that the flower becomes on the whole, bell-shaped; but it is possible that light and heat exercise some influence as regards this point. The flower is not infrequently somewhat irregular, some of the petals being smaller than the others. The petals grow decidedly during the flowering period; they are 6—10 mm long, but vary in length relatively to the sepals. The anthers and the stigmas attain almost the same height and are functional at the same time; as all the stamens simultaneously stand erect closely around the pistil, and the styles are more or less outwardly curved, self-pollination is inevitable (Fig. 27, *B*), and the numerous pollen-grains which are sometimes seen upon the styles (Fig. *C*) are also indicative of this; contact has also been directly observed (Fig. *B*). In fully developed buds the anthers are quite ripe, and they often dehisce immediately after the bud has been artificially opened; I have even found them dehisced in the bud itself, and as the stigmas also are fully developed, I

do not doubt that as a rule self-pollination takes place immediately after the opening of the bud. The stigmatic papillæ extend almost to the base of the styles; the latter

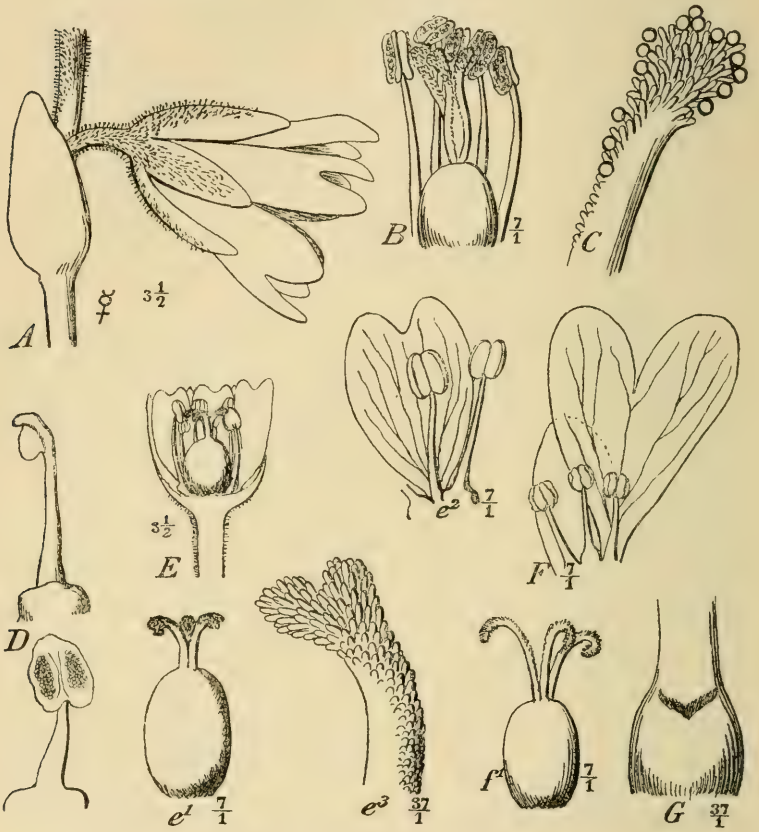

Fig. 27. *Cerastium trigynum.*

A—*C*, from West Greenland (gathered partly by Rosenvinge). *A*: ☿; length of petals 7—8 mm; styles erect. *B*, *C*: Parts of the same flower; self-pollination (6. 8. 1884).

D—*E*, from East Greenland (P. Eberlin; 30. 7. and 5. 8. 1885). *D*, Two abortive stamens; one contains some pollen. *E* with e^1—e^3: a remarkable, small-flowered form; all the cal.-st. are open and are partially empty; cor.-st. still full of pollen, but are in the act of opening.

F, *G*, from Norway (Tromsö). *F*, f^1: ♀ with quite transparent anthers which are, however, almost normal in form. *G*, base of a stamen.

are usually somewhat club-shaped, becoming broader at the apex, or even 2-lobed (Fig. 27 *C*; e^3). According to Lindman the flower has a sweet perfume (Dovre), in Greenland I made the note "White, scentless."

A remarkably small-flowered form was gathered by P. Eberlin in East Greenland (Kutek; 5. 8. 1884); it is figured in Fig. 27, *E*. The petals are in their last stage only 6 mm long and of the same length as the calyx.

♀ occur, but rarely, as far as I can see. I have seen specimens from East Greenland, the stamens of which are shown in Fig. *D*, but as some of the stamens appeared to be normal, these flowers were consequently perhaps not purely ♀.

Gynomonoecism: In the same tuft I found ☿ and ♀ with large rudiments of stamens.

Fruit is set in Greenland, for instance at 67°—70° N. lat. A ♀ was found pollinated, so that insects must certainly be of assistance there.

Norway. Gynodioecism (Tromsö, 21. 7. 1885); ☿ homogamous (West Finmark; Dovre; Tronfjæld); in all its parts as in Greenland. — ♀ has sometimes clear, transparent anthers, devoid of pollen, sometimes less decidedly reduced, and the same plant may show diversity of floral condition (Fig. 27, *F*). —Lindman: Homogamy, regular self-pollination.

I found transitional forms from ☿ to ♀ near Hammerfest, for instance, three rudimentary cal.-st., the rest normal; but I found cal.-st. < cor.-st. in a flower which occurred on a plant which had otherwise entirely ♀ flowers. In ♀ flowers I have most frequently found the cal.-st. to be the shortest. ☿ also occurred in which the stamens were so short that the backwardly-bent styles were not in contact with them, and in several ☿ the cal.-st. were < cor.-st.; but the contrary is the rule.

The Alps. Homogamy; in unfavourable weather self-pollinating to a high degree; specimens with partially shrunken stamens occur (H. M.). Italy. Homogamy (Ricca). — The flower appears to be exactly similar everywhere. Abortive stamens have hitherto been recorded only from Greenland and Norway.

5. Cerastium vulgatium L. (C. *triviale* Lin Nr.)

Denmark. Gynodioecism. ☿ slightly protandrous or almost homogamous; self-pollination takes place by the stigmas coming into contact with the anthers of the erect stamens. Sometimes all the cal.-anth. may be open, while the styles are still rolled up in the middle of the flower. The stamens usually stand more or less erect, especially the cal.-st. The anthers are white. The flower varies in diameter according to its age; at first it is about 5 mm in diameter, and afterwards as much as 8 mm. The styles bend to the right in the flower.

In a few cases protogyny appears to occur.

♀ with stamens aborted in varying degrees, some about 2 mm long, with rather large and almost normal anthers, others only 1—$1^1/_2$ mm long with transparent anthers which are, however, somewhat normal in form. Styles large, twisted (to the right), papillose down to their base, and filling the throat of the corolla. The corolla somewhat smaller than in ☿, the petals being $3^1/_2$—$4^1/_2$ mm, while those in ☿ are 5—7, most frequently 5—6 mm. The pistil is not, on the whole, more vigorous than in ☿, if anything smaller; the ovary is about 2 mm long in both. ♀ plants are rarer than ☿.

Specimens with partially aborted stamens occur.

Iceland (Reykjavik; 1884). Gynodioecism. ♀: petals 5 mm, cal.-st. 3 mm, ovary 2 mm and styles 2 mm. Some flowers had normal anthers, that is, they opened and contained pollen, which, however, appeared to be almost useless.

Sweden. Slight protandry; fertilized by self-pollination (Axell). Germany. Gynodioecism; Gynomonoecism. Slight protan-

dry, rarely pure homogamy (H. M.; A. S.); in Riesengebirge A. Schulz observed in the same individual both decidedly homogamous and entirely protandrous flowers; entirely ♀ are said to be rare. — This species is one of those in which ♀ flowers seem to be rare; they are not much smaller than the ☿ flowers.

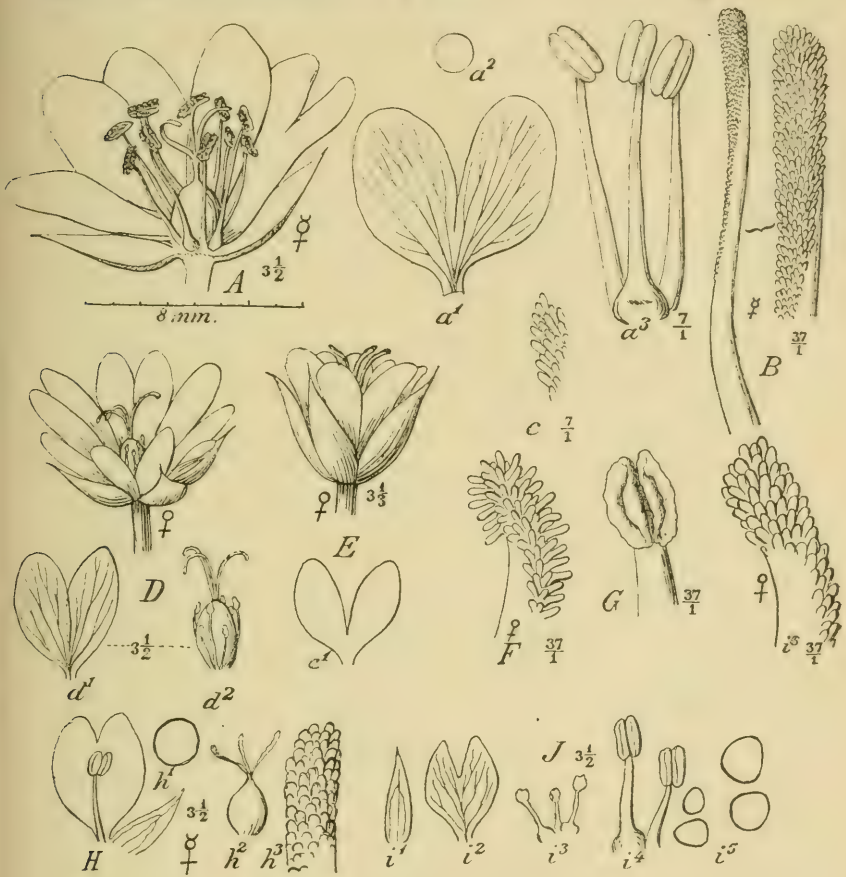

Fig. 28. *Stellaria longipes.*

☿. — *A*, from Greenland (about 69° N. lat.); a^2, pollen grain. *B*, from ☿ in its last stage. (differently magnified). *C*, Most fully developed papillæ from ☿ observed by me.

♀. — *D*, d^1, d^2, and *E*, e^1: ♀ flowers from West Greenland (about 67° N. lat.). *F*: Stigmatic papillæ of ♀ (longer than those of ☿ shown in *C*); from Greenland (about 67° N. lat.). *G*: Cor.-st. of ♀ from about 69° N. lat.

H, h^1 (Pollen), h^2 and h^3 from ☿ from Spitzbergen. *J*, i^1—i^6, from ♀ from Spitzbergen. (E. W.)

6. **Stellaria longipes** Goldie (*St. Edwardsii* R. Br.) Fig. 28.

Greenland. Gynodioecism; ☿ > ♀. Slightly protandrous or homogamous flowers.

☿ appear to be more or less decidedly protandrous or decidedly homogamous. The specimen figured in Fig. 28, *A* had all its anthers open, but the stigmas were still unripe. In the fully developed flower the stamens stand at a distance from the pistil, so that the anthers are not in contact with the stigmas which are never markedly revolute. The flower secretes honey abundantly. I am not prepared to say whether self-pollination takes place regularly, but judging from the position of the parts of the flower, there does not appear to be anything to prevent this, and the anthers are not empty when the stigmas ripen. The stigmatic papillæ extend half the distance down the styles (Fig. 28 *B*). The number of the styles varies, being sometimes as many as four.

♀ occur as far north as Upernivik (about 73° N. lat.), according to material gathered by C. RYDER (3. 9. 1886). They are much smaller than ☿ (compare Fig. 28, *D* and *E* with *A*, or, for instance, the petals d^1, e^1 with a^1); while ☿ is as much as 13—14 mm in diameter, ♀ is only 7—10 mm; the petals of ☿ are 7—$7^1/_2$ mm, of ♀ 5—6 mm. But otherwise the ♀ flowers vary as regards the relative size of the parts. Specimens occur in which the petals are longer than the calyx, others in which they are of equal length. The stamens (Fig. *G*) are smaller than, or at most of the same size as the ovary (Fig. *D*). The pistil is so large in proportion to the corolla that the apices of the styles protrude (Fig. *D*, *E*). The stigmatic papillæ are longer in ♀ than in ☿ (Fig. *F* and i^6 compared with *B* and *c*). I have no note of having seen ripe fruit from Greenland.

Spitzbergen. Gynodioecism; ☿ > ♀ (Fig. 28, *H* and *J*). It is remarkable the small size which the flowers (some-

times?) attain here, which can be seen by comparing Fig. *H*—*J* (from Spitzbergen) with the others which are from Greenland. The anthers and pollen-grains however are almost equal in size (see a^2 and h^1). The petals in some of the specimens investigated were less deeply cleft than usual (Fig.

Fig. 29. *Stellaria graminea.*

A, *B*, from ☿ from Altenfjord, gathered late in the evening of 14. 7. 1885. Markedly protandrous, the stigmas still far from ripe. *C*—*J*, from Denmark. *C*, *D*, *E*: ☿. *F*: Intermediate form. *G*, *H*, *J*: ♀ (Scale given applies to *A*, *B*, *C*, *E*, *F* and *H*). (E. W.).

H, i^2). ☿ are protandrous, the corolla is > the calyx (Fig. *H*). — ♀: the length of the corolla is equal to that of the calyx (Fig. i^1 and i^2), about 4 mm. The stamens may have rudimentary pollen-grains of varying size and form (Fig. i^5,

some are perhaps sometimes normal); but in the highest degree of reduction the anthers are transparent, without the least trace of pollen-grains. The stigmatic papillæ are also here longer than in ☿ (see Fig. i^6 and h^3).

7. Stellaria graminea L. p. p. (Fig. 29).

Denmark. Gynodioecism; ☿ > ♀, distinctly or less distinctly protandrous.

☿: Protandry, with the stamens performing movements towards the middle of the flower and back again. The anthers turn more or less outwards or even backwards. As a rule self-pollination may ultimately take place, but I have seen flowers which had lost their anthers before the styles spread out. The anthers are flesh-coloured or become ultimately somewhat brownish, the pollen is yellow in colour. The styles are covered with stigmatic papillæ along the upper $^3/_4$ of their length (Fig. 29, *G*). At first they are bent inwards or almost rolled up, ultimately spread out, scarcely rolled backwards. The flower varies greatly in size and length relatively to the calyx (Fig. *C* and for instance *E*); this is also still more noticeable when compared with flowers from other countries, for instance Fig. *A* from Finmark.

♀ appears to be as common as ☿. Its size relatively to ☿ is seen by comparing Fig. 29, *H* (♀) with *C* and *E*. The petals in ♀ are $3^1/_2$—$4^1/_2$, rarely $5^1/_2$—6 mm; in ☿ 5—7. ♀ is about 5—6 mm in diameter, while ☿ is 9—13 mm, but near Copenhagen ☿ are found which measure $3^1/_2$—4 mm in diameter, and have petals $2^1/_2$ mm in length, i. e. smaller than the calyx. It should be borne in mind that the petals grow in size during the flowering period. In some of the flowers the anthers (Fig. *J*) are quite transparent with crystals of calcium oxalate, in others the anthers are of a yellowish colour, or only their one-half is so coloured, and

pollen has begun to develop within them. Several variations may be found in the same tuft. The styles project beyond the corolla.

Intermediate forms are often found in which a few or several stamens are aborted, and the others are normal (Fig. *F*).

There does not seem to be much difference between the stigmatic papillæ of ☿ and ♀ (Fig. 29, *D* and *G*).

Norway (Altenfjord). Gynodioecism, ☿ > ♀. Protandry. ☿: petals about 5 mm; corolla when approaching 3rd stage 9—10 mm in diameter.

A particularly large form is shown in Fig. 29, *A*.

8. Stellaria media (L.) Vill.

I have occupied myself very little with this species as I expect it to be fully treated by another writer. The following is for the most part taken from the literature on the subject.

The flowers open and close according to the weather; Vaucher states that the flower lasts for one day only. Gynodioecism, Gynomonoecism. ☿: Protandrous in various degrees, self-pollination found especially in plants which flower during winter. As is well-known it flowers all the year round, even during the whole of autumn and winter, and sets fruit continually, probably in the closed flowers, thus forming a transition to cleistogamy (as regards *S. Boraeana* Jord., which is said to be a form of *S. media*, see A. Schulz; it is cleistogamous, with petals either small or absent, like *S. media* var. *brachypetala*, and with 2—3 stamens). Here self-pollination appears to give excellent results.

The flowers vary considerably in size and in the length of the petals relatively to the calyx. Lange mentions a form *apetala*. Some of the flowers, viz. the largest, have all the

Fig. 30. *Stellaria humifusa.*

☿: *A—F*, *L*. ♀: *G—K*.

A—C: ♀ from Greenland (about 68° N. lat.). *D*, Parts of ☿ from East Finmark. *E*, dimerous pistil with ripe stigmas, e^1 (Greenland). *F*, Different parts of ☿ from East Greenland (P. Eberlin); protogynous, the anthers not yet opened, but the stigmas well-developed. (The petals vary somewhat in form, which is an unimportant detail; in the same glass, specimens were found with petals of the usual forms).

G: from West Greenland (about 67° N. lat.); ♀. *H*, from the same place, larger ♀ flower (compare the two flowers, both mag. $3^1/_2$; also compare h^1 with g^1). *J*, from Greenland. *K*, from West Greenland; ♀ with stamens abortive in various degrees; pollen-grains formed in the three largest anthers, but thick-walled and irregular in form (k^1).

L: ☿ from Spitzbergen (Nathorst; 6. 8. 1882). (E. W.)

10 stamens. But the number is reduced in the smaller flowers and especially in those that flower during autumn and winter; it is in the first instance the cor.-st. which are subject to this reduction, but afterwards the cal.-st. also often share the same fate, so that the number of functional stamens may be as few as two (H. M. in Weit. Beob.). But the nectaries of the suppressed cal.-st. usually remain. According, however, to Vaucher and A. Schulz the nectaries may also vanish, or, at any rate, they fail to secrete honey, even if present.

Bennett and others have shown that they are self-fertilizing during winter or in cold weather and so display a transition to cleistogamy.

♀ are rare according to A. Schulz. According to Loew a few ♀ are to be found on hermaphrodite plants.

West Greenland (about 65° N. lat.). Appear to agree exactly with European forms.

9. Stellaria humifusa. Rottb. (Fig. 30).

West and East Greenland. Gynodioecism; gynomonoecism, ☿ > ♀; protandry, as a rare exception protogyny (East Greenland), then homogamy.

☿. Protandry with the ordinary movements of the stamens and styles; the cal.-anth. open immediately on the flower expanding. The anthers turn transversely (Fig. 30, *C*). But as a rule homogamy no doubt ensues very soon, and the backwardly bent styles are in contact with the anthers. Protogyny has been observed in specimens from East Greenland (Fig. 30, *F*, f^1—f^3); the petals were, in addition, less deeply cleft than is ordinarily the case. The styles may number from 2 to 4 (Fig. *E*); in consequence of the long stigmatic papillæ at the apex they are rather club-shaped both in ☿ and ♀. The papillæ extend about $^1/_2$ or $^2/_3$ way down the styles.

♀ are considerably smaller than ☿ (compare Fig. *A* (☿) with *H* and *G* (♀). The petals are 3—5 mm in ♀, but $4^1/_2$—5—6 mm in ☿ (sepals 4 mm). The diameter of the ♀ is 5—6 mm, but that of the ☿ 7—12 mm. The smallest of the ♀ flowers (from about 67° N. lat.) is figured in Fig. *G*; the sepals and petals are about $2^1/_2$ mm in length. The stamens have transparent, quite empty anthers; a few may be found with worthless pollen (angular, thick-walled and smaller than is normal; Fig. *K*, k^1). The nectaries are not reduced in size (Fig. *K*). The stigmatic papillæ are longer in ♀ than in ☿ (see Fig. i^1 and e^1). The ovaries are equal in size (see Fig. h^3 and d^1), or smaller in the ♀ (see Fig. g^2 and d^1). I have noted down a single case of gynomonoecism (Godhavn).

Intermediate forms occur with a few or several abortive stamens and the rest normal; as for instance one normal and nine barren. In Fig. *K* there are three anthers which are apparently normal (one cal.-st. and two cor.-st.), but the pollen-grains are thick-walled and irregularly angular (k^1).

I have not observed any fruit which had set; it is possible that the species has compensation in its profuse vegetative shoot-formation.

Norway. Protandry with ensuing homogamy; the styles become functional almost simultaneously with or a little after the cor.-st. (Altenfjord, 10. 7. 1885).

Russia (Kola). ☿: petals $4^1/_2$ mm, slightly longer than the sepals. Diameter about 7 mm. Slight protandry with ensuing homogamy.

Spitzbergen. Gynodioecism. The very small flowers which occur here are remarkable. In Fig. 30, *L* are shown parts of a ☿ with the same magnification as *A* and *C*. Sepals and petals are here somewhat more than 3 mm. Pistil small with rather erect styles, which have papillæ only at their apex. The anthers are normal, open. Can this be a form transitional to ♂? An equally small ☿ has been found in Greenland. The ♀ flowers are even somewhat smaller; the sepals and petals $2^1/_2$ mm, but the stigmatic papillæ upon the slender styles are almost of the usual length. Th. Fries states also that the flowers are smaller and the petals narrower in specimens from Spitzbergen than in those found on the coasts of Finmark.

10. Stellaria borealis Bigel. (Fig. 31).

Gynodioecism. Homogamy, self-pollination. 3, 4, 5 styles (Fig. 31, *C*, *E*). Perigynous (Fig. *A*, *G*).

Greenland (about 65° N. lat.). ☿: Corolla absent. The whole flower 3—4 mm in diameter. Homogamy. Peculiar to this species are the long styles which curve backwards and are thrust among the stamens, so that they touch the anthers (Fig. *A*, *C*, *E*); the styles have stigmatic papillæ down to their base (Fig. *D*). Sometimes 1—3 stamens are abortive. In specimens from Greenland, collected by Rosenvinge the anthers were attacked by *Ustilago antherarum* and the pistil was checked in its development.

Norway (Dovre, Altenfjord). Homogamy. ☿: Diameter as in Greenland, sometimes as much as 5 mm. Petals most frequently absent, but they may be present and are then much smaller than the sepals. Stamens 10, with palish-brown anthers. Self-pollination as in Greenland, the styles being directly in contact with the anthers.

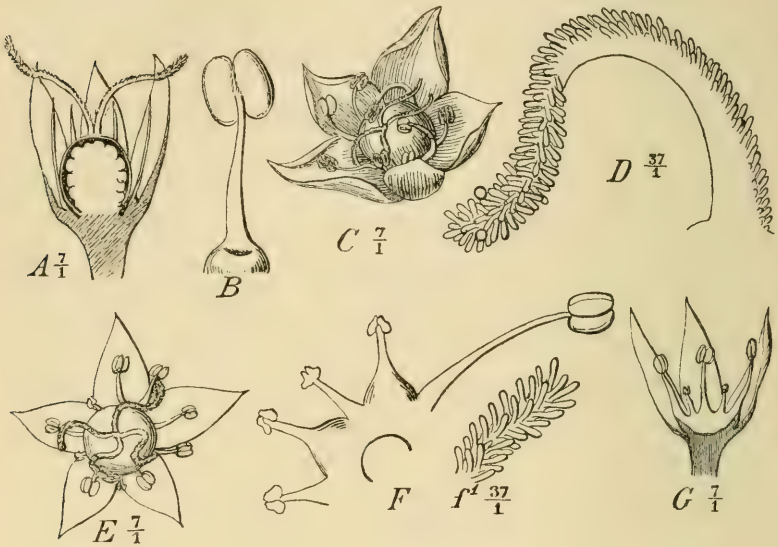

Fig. 31. *Stellaria borealis.*

A—*C*: ☿ from Greenland. *D*: ☿ from Dovre. *E*—*G*, from Kola (Dr. Brotherus).

A: ☿, the anthers have fallen off. *C*, Nine anthers have opened and are partially in contact with the widely outspread styles. *E*—*G*, A few or several stamens abortive. (E. W.).

Russia (Kola, material from Dr. F. V. BROTHERUS). Fig. *E*, *F*, *G*). Agree with those mentioned above, were also devoid of corolla. But there occurred in addition:

♀ and forms intermediate between ☿ and ♀ with stamens partially abortive; in Fig. *F*, they were all abortive excepting one (a cor.-st.); in Fig. *G*, the cor.-st. were abortive. The nectaries were not reduced, even when the filaments

and anthers were reduced (Fig. *F*, *G*). The styles have perhaps somewhat larger stigmatic papillæ than in ☿ (compare f^1 and *D*).

According to Lindman, in Norway and Sweden, *Stellaria Friesiana* Ser. var. *alpestris* Fr. greatly resembles *S. boreale* on account of its long styles, papillose a long way down; but it is either protandrous or protogynous. Self-pollination takes place easily.

Sagina. Linnæi Presl.

My own investigations are too incomplete to be recorded. Ludwig records gynodimorphism ("undeutlich"). A. Schulz records that there are two forms which differ as regards the size of the flowers. a: *decandra* Fenzl (*macrocarpa* Rchb.), petals = or slightly > than sepals. Most frequently 10 stamens. Homogamy and self-pollination. ♀ occur singly. — b: *micantha* Fenzl. which is, for instance in Riesengebirge, much commoner than *decandra*; the petals not even half as long as the sepals. Some, but rarely all, of the cor.-st. are always undeveloped. ♀ occur singly. Pollination often takes place in the closed flower. The flower is closed during dull, rainy weather, and even then self-pollination takes place with good result; consequently, this form approaches cleistogamy. See also A. Schulz in "Sitzungsber. naturf. Freunde", 1888, no. 4, p. 184, where he states that in 1886 he was staying several weeks in Hampelbande, but never saw an expanded flower, although several patches of ground were thickly covered with the plant; and the same was the case in 1887 "im westlichen Theile des Gebirges." Forma *decandra*, on the other hand, had always open flowers. — In Greenland it sets entirely ripe fruit.

11. Sagina procumbens L. (Fig. 32).

The flowers do not open in dull or in cold weather.

Denmark; Greenland. I have figured some Greenland specimens in Fig. 32, *A*—*E*, for comparison with our European specimens.

☿: Petals, small, $1^3/_4$ mm in length, smaller than the sepals (Fig. 32, *A*) which are $2^1/_2$ mm in length. The cal.-st. secrete honey as usual. Both the cal.-anth. and the cor.-anth. may be found in contact with the short, slightly outspreading styles which have very long, stigmatic papillæ which extend to their base (Fig. *E*, *F*). The Greenland specimens were found full of germinating pollen, and there can

scarcely be any doubt that this is self-pollination, which I have also directly observed in Denmark; even in closed flowers I have seen (June 25th) the anthers shed a quantity of pollen on the stigmas; that self-pollination gives a good result seems to be evident from the fact that every flower appears to set fruit with hardly any exception.

♀ I have seen from Denmark, and in Fig. 32, *F* I have figured a style which differs slightly from that of the ☿, but beyond that I have nothing further to state as unfortunately I made no notes.

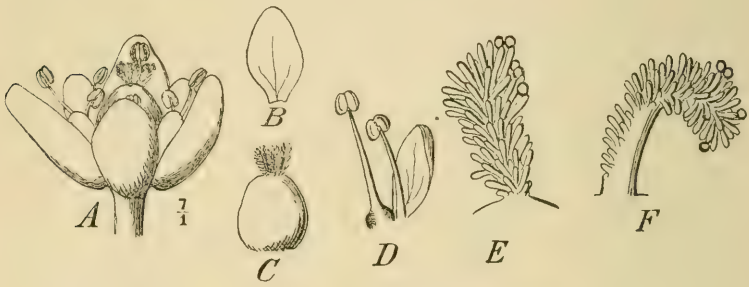

Fig. 32. *Sagina procumbens.*
A—*E*: ☿ from East Greenland (P. Eberlin).
F, from ♀ from Denmark (*E* and *F* $^{37}/_{1}$). (E. W.).

12. Sagina intermedia Fenzl.

Dovre. Pollen was found abundantly on the stigmas of styles covered to their base with long stigmatic papillæ, and appeared to have got there by self-pollination.

Fruit ripens on Spitzbergen and on the north coast of Siberia.

13. Sagina cæspitosa (J. Vahl) Lange.

Greenland (The district of Upernivik; 27. 7. 1888; C. Ryder). ☿: The petala are either equal to or < the sepals; homogamy: pollen may be found both in the anthers and

also germinating simultaneously on the stigmas. The styles are thick, short, erect and covered with long papillæ down to their base. Self-pollination principally takes place by the erect position of the stamens, whereby the anthers approach the styles. Sets fruit which ripens.

Norway (Dovre: *S. nivalis* cæspitosa?*). Gynodioecism. ♀ have small petals, and the stamens are abortive in varying degrees, as some of the anthers contain worthless pollen, and others are quite transparent. But there are also intermediate forms with some of the stamens normal and the others abortive, for instance with one normal and the rest abortive.

14. Arenaria ciliata L. (Fig. 33).

Styles 3, 4, 5.

In Greenland it sets fruit which ripens on Disco.

Norway (Alten, Skjærstad). Gynomonoecism, ☿ about = ♀.

☿: Protandry with ensuing homogamy (Fig. 33, *C* and c^1); the cor.-anth. may be partially open before the stigmas are fully developed. Stigmas and anther may be found in contact. The cal.-st. are rather erect, and the cor.-st. are also bent somewhat inwards; they are almost equal in length (Fig. 33, *C* and c^1). The styles are covered with stigmatic papillæ along their upper $^2/_3$ part. They ultimately bend so decidedly outwards that they reach across the flower, but at that time the anthers are probably always empty (Sakkabani, Alten; 10. 7. 1888). ♀ were found in a tuft together with ☿ flowers, although not with perfect anthers; ♀ do not differ constantly from ☿ as regards size (see Fig. *E* and a^2) and have three outspreading styles (Fig. *G*). ☿ in the last stage are 4—5 mm in diameter. The petals of ☿ are 4—$4^1/_2$ mm in length. The stamens of ♀ are but slightly abortive; they

are about half the size of the normal ones (Fig. *E*, *G* compared with *C*), and there is pollen in the anthers, but it does not appear to fall out and seems to be worthless. The styles appear to be stouter in ♀ than in ☿; they have in particular somewhat longer stigmatic papillæ (Fig. *F* and *D*),

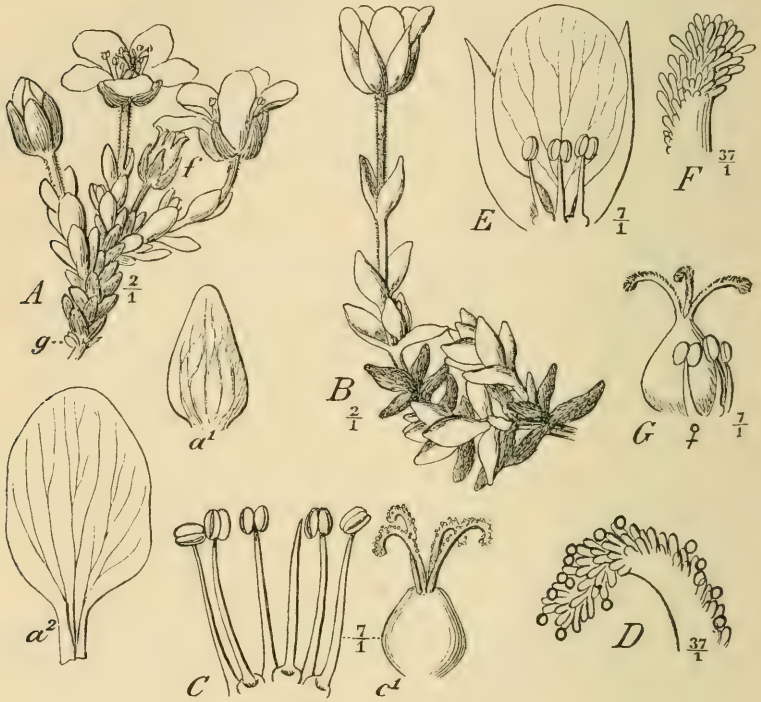

Fig. 33. *Arenaria ciliata.*

A, from Spitzbergen (Nathorst). ☿. *f*, capsule from the previous year; the darkly shaded leaves also from the previous year; *g*, a bud; a^1, sepal; a^2, petal ($^7/_1$); the latter is almost 6 mm in length.

B—*G*, from West Finmark (Sakkabani). *B*: ☿; the darkly shaded leaves are from the previous year. Flower scarcely fully expanded. *C* and *D* from ☿. *E*, *F*, *G*, from ♀. (E. W.)

but this must be verified by further investigations, the difference, as shown by the figures, being slight.

Spitzbergen (17. 7. 1882; Nathorst). Fig. 33, *A*. ☿: Appear to be protandrous. Do not differ essentially from the Norwegian specimens as regards size, and appear to agree exactly with them in other respects. MALMGREN records that the Spitzbergen specimens have larger flowers than those found in Russian Lapmark. ("Öfver. af K. Vet. Ak. Förh.", 1862).

15. Moehringia lateriflora (L.) Fenzl.

East Finmark. Appears protandrous or homogamous. Ultimately both the stamens and the styles spread out. The styles are hairy along their lower half.

16. Minuartia groenlandica (Retz.) Fenzl. (Fig. 34.)

Styles 3, 4.

West and East Greenland. ☿: Slight protandry, begins no doubt often with homogamy. In large buds I found the anthers of the erect stamens partially open and closely surrounding the erect, spreading styles, whose stigmas were not yet quite ripe (Fig. 34, *D*). But I have also observed the same position in expanded flowers, and then self-pollination is almost inevitable (Fig. *E*). The stamens and styles may be somewhat more outspread as shown in Fig. *F*, which is evidently connected with conditions of weather. The thin, white petals are 7—9 mm long and 5 mm wide, about twice the length of the sepals, which are 4 mm (Fig. *A*, *B*, *C*). Diameter 10—13 mm.

I found the seeds to be sometimes finely warted (Fig. *G*, from Ilua) and sometimes finely wrinkled (Fig. *H*, from Dronning Louise's Island). I am not prepared to say the reason of this difference, which is however but slight.

17. Minuartia biflora (L) Shinz & Thell. (Fig. 35.)

The flower is never spread out in a decidedly stellate manner because the sepals keep very erect (Fig. 35, *A*, *B*). Gynodoecism (or Gynomonoecism?); ☿ = ♀.

West Greenland (about 69° N.lat.). ☿: Slightly protandrous, perhaps entirely homogamous. In a flower like

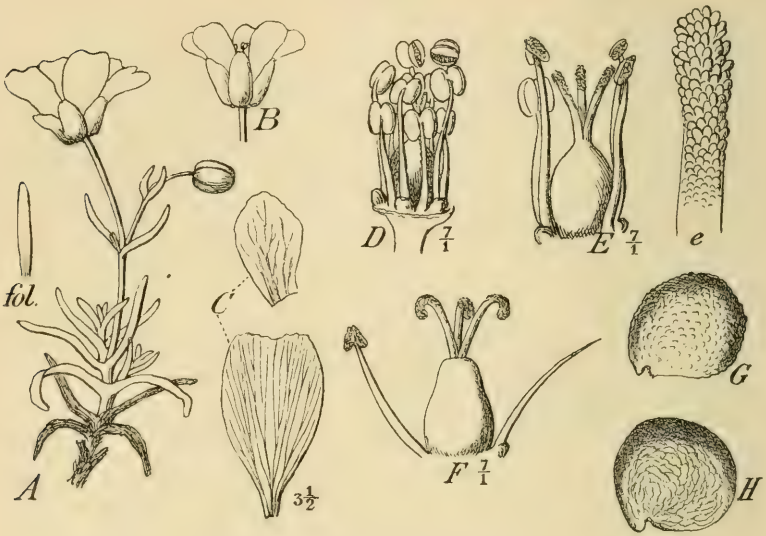

Fig. 34. *Minuartia groenlandica.*
All from Greenland. *A* (about 1½) with a leaf (*fol*) from Umanak (Rosenvinge). *B*, from Sukkertoppen (*idem*). *C*, Sepal and petal. *D*, from a bud, two cal.-anth. have opened. *E*, *e*: All the anthers have opened with the exception of three cor.-anth. (here, as is so often the case elsewhere, a shrinking of the anther-wall takes place, on dehiscence, which must aid in the shedding of the pollen-grains). *F*, from an old flower, East Greenland (P. Eberlin). *G* and *H*: Seeds from Ilua in South Greenland (Mrs. Lundholm) and from East Greenland (P. Eberlin). — (E. W.)

the one figured in Fig. *C*, the cal.-anth. only were open and shed pollen directly on the stigma (Fig. c^1). A similar flower with higher cal.-st. is shown in Fig. *E*. When afterwards the cor.-st. also open they are of about the same height as

the cal.-anth., and at a level with the apices of the styles. The anthers and stigmas are often in intimate contact with each other, the styles being thrust among the anthers; and self-pollination is inevitable. The filaments become ultimately more spreading. In some of the individuals the petals are narrow, almost spathulate, in others obovate (Fig. *D*, *F*);

Fig. 35. *Minuartia biflora.*
From Greenland. *A*—*E*, Parts af ☿.
From Norway. *F* (Altenfjord), f^1 and f^2 from ♀. *G* (☿ which has finished flowering) and *H* (seed) from Dovre.

they are rounded at the apex, and frequently emarginate or slightly toothed (Fig. *D*). The sepals are 5 mm in length, and the petals 7 mm; in a flower from Finmark the sepals were only $3^1/_2$ and the petals $4^1/_2$—5 mm long.

It seems that slight protogyny may occur, as the stigmatic papillæ may be fully developed even in the bud,

and I have seen pollen-grains retained, but not germinating, on the stigmas of a Greenland specimen, the cal.-anth. of which were on the point of opening.

Fruit is set in Greenland, as it seems regularly and abundantly, at least as far as 70°—71° N. lat.

Norway (for instance Altenfjord, about 70° N. lat.). Gynodioecism.

☿: Slight protandry, as the cal.-st. bend inwards towards the middle of the flower and open their anthers over the still unripe styles; or homogamy and self-pollination; the anthers may be found full of pollen at the same time as there is germinating pollen upon the stigmas, and they may be found in contact with the latter. It is possible that protogyny also occurs.

♀: All the anthers abortive, but in various degree; they may be found to be shrunken; brownish, without any pollen at all, but with indications of the four pollen-sacs, as there is a transverse fold in each half (Fig. *F*, f^1). ♀ = ☿ as regards size, but the stigmatic papillæ in ♀ appear to be constantly longer than in ☿ (Fig. f^2 and c^1), and perhaps the pistil is, on the whole, somewhat larger, but this I have not measured precisely. A young fruit and a seed is shown in Fig. *G* and *H*. — LINDMAN finds that they correspond with those of the Alps.

Spitzbergen. Appear to agree with Greenland specimens, but the flowers appear to be smaller (sepals $3^1/_2$ and petals $4^1/_2$ mm). In the specimens from Spitzbergen the anthers were on the point of opening even in the bud, and scarcely has the flower expanded, when the anthers dehisce. — Sets ripe seeds.

18. **Minuartia stricta** (Sw.) Hiern.

Greenland. The plant evidently sets ripe fruit regularly, at least as far as 70°—71° N. lat.

Norway (Dovre). Homogamy prevails at least for a time, and as the anthers are at a level with the three highly papillose styles, and as fruit is so abundantly and regularly set, I must presume that self-fertilisation of the small flowers takes place with good result.

Fig. 36. *Minuartia verna* (L.), *var. hirta* (Wormskjold).

From Greenland (Disco, about 69° N. lat.). *A* with a^1 (foliage leaf $^7/_1$), a^2, a^3 and a^4.

From Norway. *B* (Altenfjord) and *C* (Dovre; 14. 7. 1887), c^1 and c^2 (seed).

From Spitzbergen (Nathorst; 1. 7. 1882). *D* (E. W.).

19. Minuartia verna (L.) Hiern.var. **hirta** (Wormskjold). (Fig. 36).

Styles 3, 4.

Greenland (about 69° N. lat.). A specimen, twice magnified, is shown in Fig. 36, *A*; the length of the petals is almost equal to that of the sepals. ☿: Self-pollination and no doubt decided homogamy. Sets fruit which ripens.

Norway (Dovre, Altenfjord, about 70° N. lat.). The petals may be still shorter than in the Greenland specimens (Fig. *C*, *D*); sepals $3^1/_2$, petals $2^1/_2$—3 mm; the entire flower may attain a diameter of 5 mm. Specimens from Alten have petals only about half as long as the sepals (Fig. *B*). — ☿: Homogamy. In younger flowers the stamens stand erect with the anthers gathered closely above the styles, and pollen is found simultaneously in the anthers and germinating on the stigma. Finally, the styles curve backwards, and can even then touch the anthers (Fig. a^3, c^1, *D*). Self-pollination may take place easily. Fruit is set abundantly. A seed is shown in Fig. c^2; it is finely wrinkled.

A specimen from Norway (Foldal) appeared to be protogynous; the styles were spread out and were quite ripe, all the anthers were closed and stood at a lower level than the ovary, perhaps this was a ♀, or a form transitional to it. — I have seen ☿ only.

Spitzbergen (Fig. *D*). The specimens preserved in alcohol which I have investigated, had their flowers closed, and were homogamous; the open anthers stood at a level with, and were probably pressed closely against, the styles which were somewhat curved backwards (Fig. *D*); there was a rather large quantity of pollen on the stigma (Fig. *D*), so self-pollination had no doubt taken place there. Ripe fruit was developed; the seeds resemble exactly those from Dovre. The capsule is only very slightly longer than the calyx.

20. **Honckenja peploides** (L) Ehrh. (Fig. 37.)[1]

Styles 3, 4, 5 (6). 4-merous and 6-merous flowers occur (Fig. 37, *G*), for instance with 6 sepals, 6 petals, 6 + 6 stamens, 4 carpels.

[1] I do not think there is sufficient cause to place this species in a separate genus (*Ammodenia* Gmel., a name older than *Honkenya*

Greenland, Iceland, Spitzbergen, Nova Zembla, Norway and Denmark. I found the flower-biology to be the same everywhere, because the many variations as regards size which are found to occur in the flowers I must regard as local, I have observed these variations to occur in flowers from all countries without it having been possible for me to formulate any rule concerning this. ♂ and ♀ flowers are common everywhere, no doubt equally frequent, while ☿ flowers are rare, perhaps even very rare, and in this North America differs markedly from Europe (see Hook. et Benth. Genra pl.).

Dioecism, polyoecism (☿, ♂, ♀), monoecism; ♂ and ☿ are > ♀.

♂ (Fig. 37, *A* —*D*, *F*—*H*). At first the cal.-st. are more erect, and in this position they open their anthers; afterwards they bend backwards and become outspread; the cor.-st. perform the same movements, but I do not think they become so erect; the anthers do not turn. The cal.-st. have very large and yellow, glistening glands (Fig. *A*, d^1, h^1, etc.) which evidently secrete honey (by the river Alten I saw a *Coccinella* search for the honey). The variations in size are very considerable (compare Fig. *A*, *B*, *C* and *D*). The sepals are $5^1/_2$—7 mm in length; the diameter of the flower is as much as 12—13 mm; petals 3—5 mm long. But in addition

Ehrh.; *Halianthus* Fr., and others), because the fleshiness of its vegetative parts and of its calyx is an adaptation-character to a saline substratum; it has no fleshy disc in "the hollows of which the stamens stand fixed," as several authors record, but simply the same glands on the cal.-st. as the other *Alsineæ* have (Fig. 37, d^1). True, there remain the large seeds, the partially many-chambered capsule, and the development of ♀ and also ♂, but as regards the kind of flower, in North America they are mostly ☿, and the capsule character varies, many small seeds may occur, and the dissepiments may disappear even during the flowering. It can at most be referred to a sub-genus under *Minuartia*.

Fig. 37. *Honckenya peploides* (L.) Ehrh.

(The magnification the same, viz. about $2^1/_2$ for *A*, *B*, *C*, *D*, *E*, *K*, *L*, and $^7/_1$ for the majority of the isolated stamens, etc.).

♂: *A*, from Greenland (about 60° N. lat.). All the stamens are open and full of pollen. Detached petal (a^1), pistil (a^2) and pollen-grain (a^3). *B*, from Denmark. *C*: ♀ from Reykjavik (about 7 mm in diam.). *D*: from Spitzbergen (Nathorst; 9. 8. 1882); about 6 mm in diam.; cal.-anth. open, cor.-anth. closed; see d^1.

☿: *E*, from Spitzbergen (Nathorst; 9. 8. 1882), taken from a branch on which was a large fruit. Sepals 5 mm, petals $2^3/_1$ mm. There was germinatiag pollen upon the stigmas; to this belong e^1 and e^2.

♂: *F*, from Tromsö, with style (f^1). *G*, nat. size, with g^1 and g^2; from Altenfjord. *H*, from Kola (Dr. Brotherus), nat. size; to this belong h^1 (one cor.-st. abortive), h^2 and h^3.

♀: *J*, from Kola (Dr. Brotherus) with i^1 and i^2; these flowers from Kola are remarkable on account of their long and pointed sepals. *K*: ♀, from Spitzbergen (Nathorst; 9. 8. 1882). Pollen rather abundant on the stigma and some of it germinating. The anthers (k^1) were quite transparent. *L*: ♀ from Tromsö; to this belong l^1, l^2. l^3. (E. W.)

the relative length of the calyx and the corolla varies, as shown in Fig. 37 (cal. > cor. in Fig. *A*, *C*, *D*; cal. = cor. in Fig. *B*); the petals may be as long as the sepals or much shorter, for instance, half as long, and examples of both kinds of flowers may be found on the same shore.

Flowers are also recorded in which the petals are entirely absent (f. *apetala*) or in which the petals have partially disappeared. The diameter of the flower varies greatly according to the degree to which the sepals have expanded, and increases during the flowering period; it varies between 7—14 mm.

The petals vary also in form, and the narrower they are, the more reduced is the venation (compare Fig. a^1, d^1 and g^2). I have not found the form in which the corolla is entirely wanting (*apetala* Rostr.). The length of the stamens varies also, relatively to the corolla and the calyx. The pistil is remarkably large, usually 3—4 mm in length and appears to be normal, but the styles are very short ($^1/_2$—$1^1/_2$ mm), almost conical, erect and minutely papillose, and they always remain so (see Fig. a^2; *F*, f^1; h^3).

The figures show also that they vary in length (the styles of a^2 are for instance much longer than those of F and h^3).

The ovary characters also appear to be fairly normal; the ovules are large, perfectly formed (Fig. 37, F) and curved, the integuments are formed, even the long hairs which serve to guide the pollen-tubes are there, but the nucellus appears to be more or less shrunken, and on closer inspection the whole conveys the impression of being abnormal. The ovules are not everywhere abortive to the same extent, even in the same ovary they may be found to vary in size, and in some cases I must even assume that the ovules had been quite normal, but fruit-setting was nevertheless impossible, because the stigmatic papillæ were so undeveloped (f^1). All these flowers die also without setting fruit, and in such withered and closed flowers the size and position of the ovary and the styles is found to be unaltered.

Near Altenfjord (Norway) I gathered unusually large ♂ flowers (Fig. 37, G): in one 6-merous flower the diameter of the calyx was about 16 mm, and the length of the petals 5 mm. As regards other features see Fig. g^1, g^2. I have gathered unusually small ♂ flowers, for instance on Sjælland: diameter only 6 mm, petals 3—$3^1/_2$ mm, cal.-st. 5 and cor.-st. 4 mm. In the latter locality the small-flowered plant was growing about 15 degrees south of the large-flowered one.

♀: ♂ flowers with a few rudimentary stamens occur, but they seem to be rare. Purely ♀ flowers are common. Here also the flowers vary considerably in size and in the relative length of their different parts, but on the whole the ♀ are $<$♂ (compare Fig. h^3 with J; as also K and L with ♂ uppermost in the plate: A—D). The diameter of the calyx is for instance 7—9 mm and that of the corolla about 5 mm, and the petals in particular are always very small, usually only 1 to 2 mm long (see Fig. i^1, k^1, l^1). The same figures show their length

relatively to the stamens. The stamens usually have very short filaments and transparent anthers, but the size of the glands is about as in ♂. The styles are 2—3 mm in length, and finally they are straight, laterally outspread and highly papillose (compare Fig. i^2, k^2 and f^1).

All the ♀ described above set fruit abundantly, at any rate in Denmark, where, consequently, insects must be present which pollinate them. Fruit is also set in West Greenland and in Iceland. I have seen very small ♀ from Spitzbergen (Fig. *K*) and Tromsö (Fig. *L*). The sepals were only $3^1/_2$ mm. There was germinating pollen on the stigma of the flowers from Spitzbergen, so there, also, pollinating insects must be present, and a female plant had fruit on it (9. 8. 1882, Nathorst).

☿ seem to be very rare; I have seen specimens only from Spitzbergen and northernmost Norway; according to my pocket-book notes they are not rare in Greenland; but as regards Greenland a confusion with ♂ is possible, and my statement in "Bestøvningsmaaden af nogle grønlandske Blomster", p. 130, needs to be revised (see however North America; note on p. 231). A specimen from Spitzbergen is shown in Fig. *E*. They are of medium size and resemble more closely ♂, but the styles are longer, outspread and more highly papillose; most likely the papillæ would have grown longer than those in Fig. e^2 as the flower is hardly yet in its last stage. As it is they stand midway between ♂ and ♀.

Monoecism. Near Molde on the coast of Norway I saw fruit on a plant on which there were also withered ♂ flowers.

The case mentioned by me in 1878 in "Bot. Tidsskrift", vol. 10, of vegetative shoots growing out after flowering and developing vigorously above the uppermost flowers, I have often observed since, for instance also in West Finmark; I have now even seen these shoots begin themselves to flower.

21. Viscaria alpina (L.) G. Don. (Fig. 38).

Styles 4—5.

West and East Greenland. Fragrant flowers (the perfume recalls slightly that of vanilla). Gynodioecism. ☿ > ♀.

☿: Protandry with the ordinary movements of the stamens and styles, in three sets, finally homogamy. Self-pollination will be able to take place. Scarcely does the flower begin to open, then the cal.-anthers are seen at the throat. The stigmatic papillæ occur only on the upper half in a continuous row, but farther down small ones occur at intervals. During the flowering period the stamens are thrust far out and are exposed, so that they are quite bared to the effects of rain and dew (Fig. 38, *A*). The pollen-grains are greenish and ordinary in structure (numerous pores; Fig. a^1).

Protogyny occurs; at first the styles spread out and then curve backwards; their papillæ are bigger than those in the protandrous flower. Then the cal.-st. spread out, and finally the cor.-st. But this is very probably a form transitional to ♀. In the same inflorescence I found both quite sterile flowers and also protogynous ones with stamens partially abortive.

♀: Seem to be much rarer than ☿. Even before the flower is fully expanded the apices of the styles project beyond the throat (Fig. *G*).

The following figures show the relation between the ☿ and the ♀: —

☿ Petals $9^1/_2$—11 mm in length.

♀ — $6^1/_2$— 8 — —

☿ Corolla about 10—12 mm in diameter.

♀ — — 7—8 — —

☿ Corolla-tube (up to the scales at the throat) 4—5 mm.

— - (— — — $3^1/_2$ mm.

In ♀ the anthers of the stamens may be quite transpa-

rent, thin and devoid of fibrous cells, but may however attain a length of 2—3 mm (Fig. *E*, *F*); or they may be fairly normal, have fibrous cells, and well-developed, but useless pollen-grains, as in the intermediate forms (Fig. c^1).

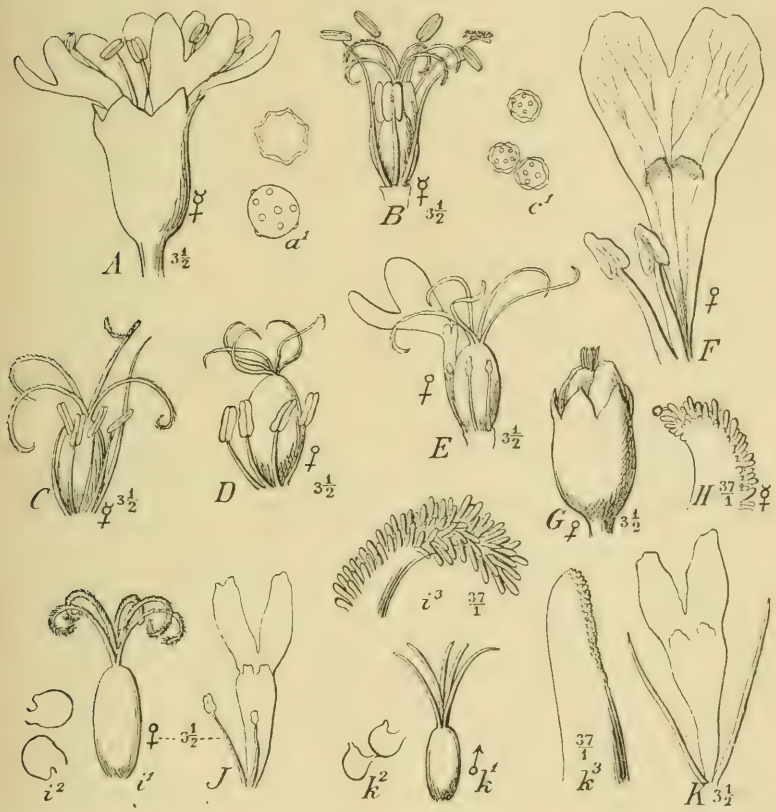

Fig. 38. *Viscaria alpina.*

A—*H*, from Greenland; *J*—*K*, from Norway (Altenfjord; about 70° N. lat.). — *A*, ☿ in its second stage; a^1 normal pollen-grains. *B*, ☿ with protogyny; cal.-st. have become outspread, but only one anther has opened. *C*, ☿, with only one normal anther; in all the others the pollen-grains are small and abnormal (c^1). *D*, ♀, with fairly normal anthers, but the pollen is worthless. The styles are withered; the ovary is evidently swollen. *E* and *F*, ♀ with transparent anthers. *G*, ♀ in a bud; the styles are already protruding. *H*, Stigmatic papillæ of ☿. *J*, i^1, i^2 (ovules) and i^3 from ♀. *K*, k^1, k^2 (ovules) and k^3 from ♂. (E. W.)

The pistil is perhaps somewhat larger than in the ☿, and the styles reach right across the petals, twisting to the left. The stigmatic papillæ are larger than in the ☿ (see Fig. i^3 and *H*).

Transitional forms from ☿ to ♀ occur, the anthers being only more or less abortive in some of the stamens, and normal in the others. Among the abortive stamens there often occur some with pollen and fibrous cells, but the pollen-grains are smaller than ordinary, thicker-walled, and of irregular outline; the pores are also more distinct (Fig. c^1). The barren stamens do not become elongated (Fig. *C*).

In a flower (Greenland, about 67° N. lat.; 13. 7. 1884) one of the cal.-anth. was seen to be open while all the others were closed, and the styles were already entirely outspread; if this was not an imperfect ☿, then there must have been protogyny (Fig. *B*).

♂. In "K. Danske Vid. Selsk. Overs.", 1886, p. 129, I recorded the occurrence of ♂ in Greenland, but I am now rather doubtful as regards this point.

Ripe fruit is commonly set in Greenland.

Norway (Dovre and Alten); Sweden (Fig. 38, *J. K*). Gynodioecism and Gynomonoecism, Andromonoecism; slightly fragrant in the evening. ☿, protandrous, corolla-tube $4^1/_2$—5 mm; diameter 10—11 mm, exactly as in Greenland.

A 4-merous flower was found together with 5-merous ones, viz. 4 seps., 4 pets., 4 + 4 st. and 3 carp. The number of the styles are 3—4—5.

♀: Diameter 7—9 mm, corolla-tube 5—$5^1/_2$. In specimens from Alten the ovaries were smaller in ♀ than in ☿, viz. $3^1/_2$ mm as compared with 4—$4^1/_2$ mm; the styles, on the other hand, were slightly longer. The petals 10 mm in length in ☿ and $6^1/_2$ in ♀. Near Alten female plants were found (15. 7. 1885) which had set numerous fruit the year before.

Andromonoecism occurs on Dovre. In a dense inflorescence the lowermost flowers were purely ♂, while the uppermost ones were more or less distinctly ☿. ♂ > ♀ (see Fig. *K* and *J*). In ♂ the petals were $9^1/_2$ mm and in ♀ 8 mm in length. In ♂ the pistil is smaller, the ovules are smaller and compressed, but appear otherwise to be fairly normal, only the stigmas are undeveloped (Fig. k^1, k^2, k^3, compared with i^1, i^2, i^3).

[Note. Lindman and Axell: Gynodoecism, ♀ common on Dovre; slight protandry.]

22. Melandrium[1] apetalum. (L.) Fenzl. (Figs. 39 and 40).

Greenland. Sets ripe fruit, at least as far as 70°—71° N. lat.

Norway (Kongsvold, Alten). ☿ and ♀.

According to Lindman dimorphous ☿, protogynous-homogamous. He has described more closely the variations which occur in the structure of the flowers: (**a**) some flowers are larger than the others, but are more inconspicuous and have shorter stamens, the petals do not reach to the throat of the calyx; they are dull dark-red (Fig. 39, *A*, A^1, a^1). The flowers are protogynous, and the styles twisted; (**b**) others are smaller, have protruding petals and longer stamens (see Fig. *D*, *C*); he regards them as approaching to ♂. The calyx is thinner and lighter coloured. The anthers stand at a higher level than the stigmas.

[1] The characters on which the genus *Wahlbergella* is founded are very insignificant, and the genus ought not to be retained; also the characters are not correct; as for instance the record in Hartmann's Flora that the claws of the petals of *Wahlbergella* are wingless, but those af *Melandrium* are winged, or that the seeds have a membranous edging; for *M. triflorum*, which evidently stands very near to the two *Wahlbergella*'s, has wingless seeds (see Fig. 41, *H*).

♀ flowers are also mentioned by LINDMAN, they belong to form a.

I have found the same forms, not only the different ☿ flowers, but also the ♀. As regards the former, reference should be made to LINDMAN's figures; I shall only remark that according to specimens which I have seen cultivated

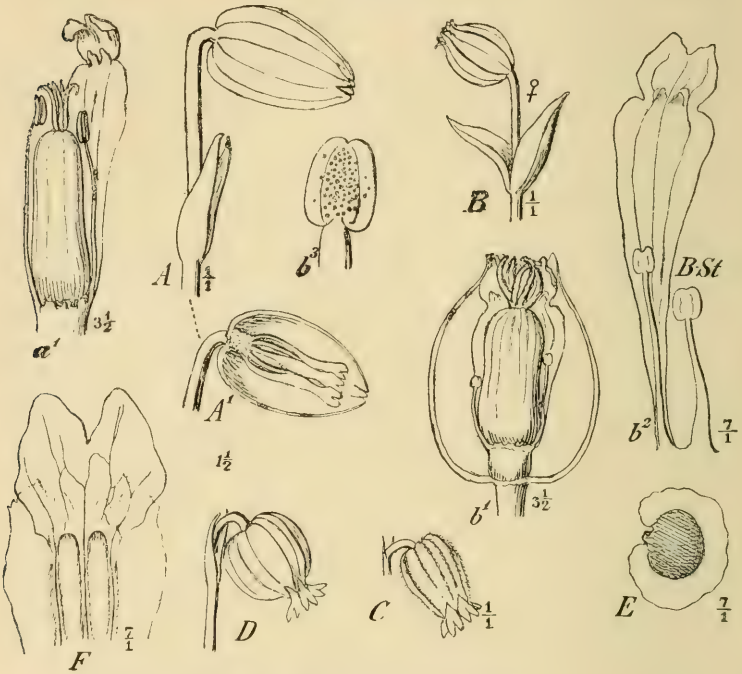

Fig. 39. *Melandrium apetalum.*
A, *A*¹, *a*¹: ☿ with short petals (f. *brevipetala*); Dovre, 14. 7. 1887 (calyx 18 mm long, petals 13 mm; cal.-st. 8—9 mm. The stigmas are covered with pollen). *B*, *b*¹, *b*², *b*³: ♀ from Altenfjord (about 70° N. lat.), 18. 7. 1885. The petals and the styles are just at the throat of the calyx (*b*¹); *b*³: anther with crystals of calcium-oxalate. *C*, *D*: Flowers from a cultivated plant (seeds from Petrograd); the petals are protruding; in *D* the calyx is greatly swollen. *E*, Seed (Dovre). *F*, Dorsal view of petal. (E. W.)

(seeds from Petrograd), there occurs a form with much more inflated calyx, becoming almost globular, even during the

flowering period; it has protruding petals (Fig. *C* and *D*). In this form the flowers do not become erect after flowering, but remain nodding. Self-pollination appears inevitable, as the anthers no doubt lie for a long time quite close to the stigma, or else the pollen falls from them down upon it; anthers may also be found which are in direct contact with the stigmas. I give a few figures of ♀ which show that the anthers may be fairly normal in form, but they are transparent, devoid of pollen and with crystals of calcium oxalate (Fig. b^1, b^2, b^3). It is smaller than ☿ (Fig. *B* and *A*); the total length about 12 mm against 17 mm; petals about 9 mm, cal.-st. scarcely 5 mm and cor.-st. 3 mm, styles 2 mm, thicker than usual (Fig. b^1). The ovary also appears larger, about 6 mm long.

Th. Fries has established a variety *arctica* ("Tillägg. til Spitzbergens Fanerogamflora" in Öfvers. of K. Vet. Ak. Förhandl., 1869, p. 133); it has protruding petals, consequently, it seems to come near to the above-mentioned form which Lindman describes as being more staminate, and is perhaps identical with it. In the flowers of this form from Spitzbergen, which I have investigated, the limbs of the petals were protruding and the anthers were standing just at the throat, at a level with the uppermost tips of the styles. They appeared to be protogynous. As an indication of self-pollination may be mentioned that pollen was found only on the upper end of the style, just where the cal.-anth. could touch it, as long as the cor.-anth. which were standing at a lower level, had not dehisced. On the other hand, in a flower in which the cor.-anth. also had dehisced, without the cor.-st. having as yet become outspread, there was also pollen on the middle of the style, separated off from that of the upper part, and its situation corresponding to the level of the lower anthers; it had not yet germinated, which,

on the other hand, the pollen situated higher up had. Thus, there was both as regards the position of this pollen and the degree to which it had germinated, every reason to believe that it came from the anthers of the same flower. For the rest, an immense quantity of pollen may be found deposited on the styles. Petals total length 15 mm, cal.-st. 10 mm long, cor.-st. 8 mm, pistil 8—8$^1/_2$ mm, of which the styles about 3 mm.

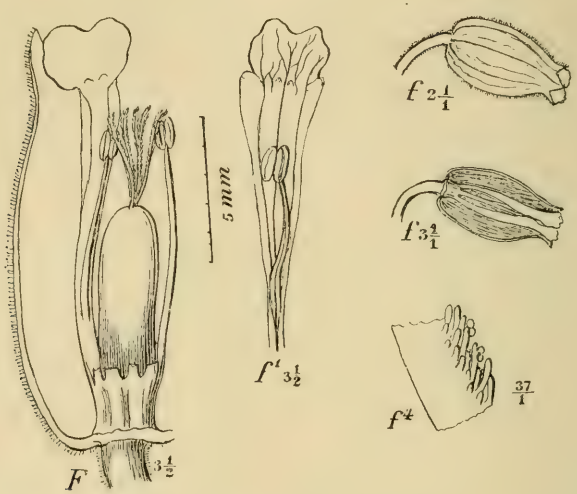

Fig. 40. *Melandrium apetalum.*
From Nova Zembla, gathered by Th. Holm. *F*, Anthers open; many pollen-grains in them, some of which are germinating. (E. W.)

I have seen flowers from Nova Zembla (Fig. 40) which in a way stand intermediate between the two forms described by LINDMAN. The petals are just visible at the throat of the calyx (Fig. *F*), consequently, they are longer than in the one of his forms, but shorter than in the other; the anthers are at the level of the stigmas; much as in one of his forms, open, and quite evidently able to carry out self-pollination. In addition, the pollen was germinating in abundance not only in the anthers, but also on the stigmas. In Nova Zembla fruit is set which ripens.

23. Melandrium triflorum (R. Br.) J. Vahl (Fig. 41).

Greenland. I have described it in "Overs. over d. K. danske Vid. Selsk. Forhandl.", 1886. Slight perfume.

☿: Slightly protogynous; self-pollinating. Both the cal.-anth. and the cor.-anth. lie finally close to the styles and are in contact with them. The styles, surrounded by

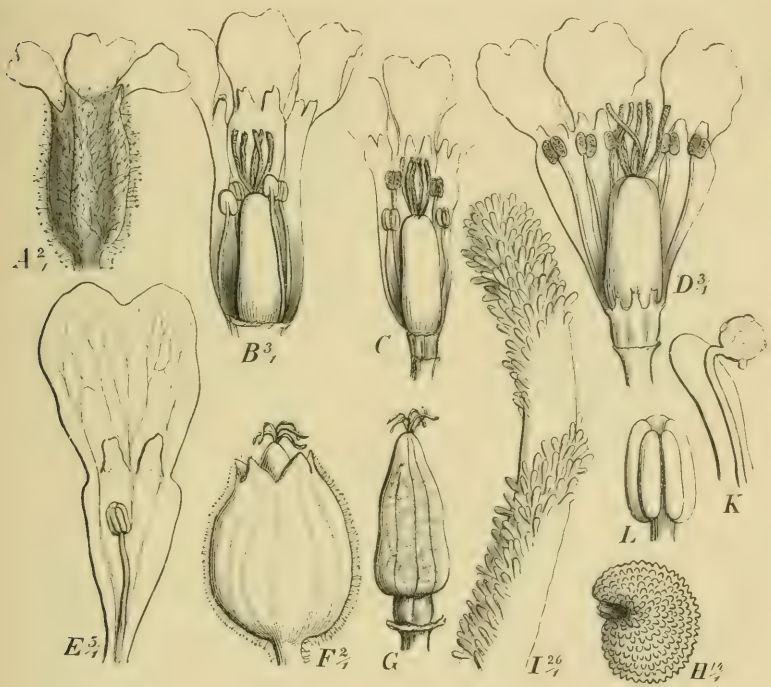

Fig. 41. *Melandrium triflorum* (R. Br.) J. Vahl.
A, The limbs of the petals are more or less outspread. The appendages of the throat (see *E*) are hollow. *B*, On the slightly club-shaped styles the stigmatic papillæ are fully developed (see *I*), but the anthers are closed and stand at a lower level than the styles. In *C* the cal.-st. have straightened, and the anthers have opened at the level of the middle of the styles, almost at the throat of the flower. In *D* the cor.-st. have also straightened and opened their anthers (the parts of the flower are spread out artificially). As the stigmas are still ripe, self-pollination will certainly be inevitable. In flowers at this stage of development I always found a great quantity of pollen on the stigmas, partially germinating (*K*). *F* and *G* almost ripe fruit. *H*, a seed. Some of the hairs have been omitted. From Kristianshaab, W. Greenland. (E. W.)

the anthers, are situated just at the narrow throat. A large quantity of pollen-grains may be found on the stigmas, some of them germinating. Six styles may occur. Petals 12—12$^1/_2$ mm. Throat-scales hollow. Dehisced cal.-st. 8$^1/_2$ mm, pistil 7$^1/_2$ mm to the tip of the styles. Diameter of corolla 12 mm finally. Fruit appears to be set very regularly. (See expanation of Fig. 41).

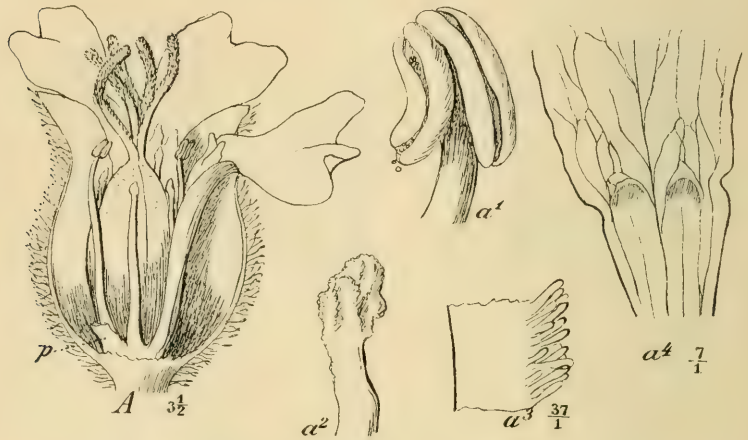

Fig. 42. *Melandrium triflorum.*
From Greenland (about 73° N. lat.; C. Ryder, 5. 7. 1887). Parts of ♀; a^1 and a^2, anthers showing different degrees of reduction. a^4, Dorsal view of petal.

I have received ♀ flowers of this species also, gathered by Lieut. C. RYDER at about 73° N. lat. in West Greenland; one of them is illustrated in Fig. 42. Four of its cor.-st. contain a little pollen, but it is not normal; in another flower only one or two of the cor.-st. contained a little pollen. All the cal.-st. are smaller than the cor.-st. and more reduced. Petals 13 mm, cal.-st. 6 mm, cor.-st. 8$^1/_2$ mm, styles 5 mm, diameter of corolla 8—10 mm.

Transitional forms from ☿ to ♀ occur with a few or several anthers developed, for instance, all the cal.-st. sterile, and all the cor.-st. normal and longer than the cal.-st.

In Greenland fruit is set which ripens even as far north as 76° N. lat., and fruit-setting appears to begin very early.

24. Melandrium affine J. Vahl.

(See Warming in "Oversigt over D. Kgl. Danske Vidensk. Selsk. Forhandl." 1886, p. 129).

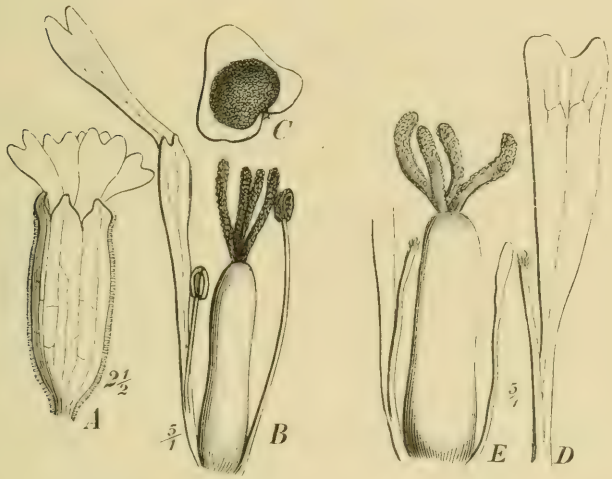

Fig. 43. *Melandrium affine* J. Vahl.
A, *B*, Hermaphrodite flowers. *C*, a seed. *D* and *E* from male flowers; the filaments are developed, but not the anthers, and the petals differ in form from those of ♀. From Altenfjord, northern Norway. (E. W.)

Greenland. ♀: Slight protogyny. Self-pollination. Calyx 12 mm, corolla-tube about 10—11 mm, cal.-st. $9^1/_2$ mm, cor.-st. $8^1/_2$—9 mm. The calyx-anthers reach to the tip of the styles. The anthers shed masses of pollen upon the stigmas, with which they are in direct contact. Petals white. Sets ripe fruit in West Greenland, regularly it appears, for instance at 70°—71° N. lat., and even as far as Grinnell Land (Discovery Bay, according to a specimen from the

Herb. Upsala, which was forwarded as *L. apetala* L. var., but according to Th. Fries is a true *Mel. affine*).

Norway (Altenfjord, about 70° N. lat.). ☿, ♀. Protogyny.

☿: The anthers of the cal.-st. in my Fig. 43, *B* are open and pressed against the styles to which they adhere by means of the pollen tubes. The styles (4—5—6) are slenderer than in ♀; the cor.-anth. have not yet dehisced.

In another ☿ all the anthers were of equal height and at a level with the upper one-third of the styles, consequently they were all like the cal.-anth. in my Fig. 43, *B*. The stigmatic papillæ extend down to the base.

♀ (Fig. 43, *D*, *E*): The petals are narrow, smaller and less notched at the apex, and the scales at the throat are absent, the stamens sterile, either with anthers (pale, transparent) or even entirely without anthers, but terminating in long hairs. Styles 4, thick, twisted. The stigmatic papillæ are short, and fairly equal in length from base to apex. The ovary is considerably larger (both longer and thicker) in ♀ than in ☿ (Fig. *E* and *B*).

Spitzbergen (15. 7. 1882; Nathorst). ☿: Protogyny. In a well-developed bud the styles were spread out and the stigmas almost ripe, and the anthers had so far developed that the pollen-grains were lying isolated. In older flowers the stigmas were found covered with germinating pollen before the cor.-st. had elongated and opened their anthers; this pollen comes evidently from the cal.-anthers. Fruit ripens in September; also in Nova Zembla.

25. Silene inflata (Salisb.) Sm.

Flower scentless; moth-pollinated. The petals are not involute[1]).

[1]) Vaucher has a great many good biological observations on the *Sileneæ* which have not been noticed in the newer literature, for

Denmark. Trioecism and gynomonoecism; protandry. The scales at the throat consist of two low protuberances with corresponding shallow depressions on the dorsal side. Zygomorphy is often distinctly seen, the stamens and styles being bent downwards in the lower part of the flower; the flower is what Delpino calls zygomorphic of the 1st degree.

☿: Highly protandrous, the stamens appear gradually not exactly in two sets. The stamens project far out.

♂ are almost equal to ☿ in size; they are hardly common.

♀ < ☿. Diameter of corolla 13—14 mm, in ☿ 15—18 mm (the corolla grows during the flowering period), but otherwise the difference is but slight. In both flowers the calyx is 12—13 mm in length, the corolla-tube in ♀ 9—$10^1/_2$ mm, in ☿ 11 mm; petals in ♀ 13—14—16 mm, in ☿ 14—$16^1/_2$ mm, the limb in ♀ 4—5 mm, in ☿ $5^1/_2$ mm. The ovary is $3^1/_2$—5 mm in length in both; and the thickness and the length of the style are the same in both. Nor can I see any difference as regards the ovules; there are about 12 in each row, both in ☿ and in ♀. The calyx-stamens in ♀ are often remarkably long, viz. $4^1/_2$—5—$6^1/_2$ mm in length, so that they project far above the ovary, and they have distinctly marked-off, dorsified anthers; the length may diminish to 2—$2^1/_2$ mm. The cor.-st. are as usual somewhat smaller. The anthers are

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instance with regard to the involution of the petals (those that become involute in the evening he calls "meteoric corollas"); and with regard to protandry, direct or indirect pollination (e. g. self-pollination and crossing); and about movements before, under and after flowering, etc. In one place he writes as follows: — "Du reste, on peut croire qu'en observant les divers *Silene* sous ce point de vue, on y découvrirait d'autres arrangements qu'on ne soupçonne point encore, et qui donneraient une idée bien plus grande de la richesse et de la variété que le créateur à mises dans ses ouvrages, que ne peuvent le faire les differences de feuilles ou d'inflorescences".

transparent, thin and without the least indication of pollen. The styles protrude 8—10 mm and are on the whole 15—16 mm long.

LANGE indicates the female plant as f. *micropetala*.

Gynomonoecism: A few ♀ together with ☿.

Norway, Sweden: Gynodioecism. I found ♀ in Østerdalen and on Dovre, as also in the neighbourhood of Stockholm; it may have very rudimentary stamens, and the diameter of the corolla may be 17—18 mm, consequently much larger than recorded above. ☿ protandrous. Both zygomorphic. Trioecism with ☿ and ♀ > ♂ according to AXELL.

26. Silene maritima With.

Norway (Altenfjord). ☿: Rather markedly protandrous with the usual development in three sets, but the cor.-st. may spread out singly and almost simultaneously with the cal.-st. Calyx 15—16 mm in length; diameter of corolla 13—15 mm, corolla-tube about 13 mm, stamens 14 mm in length, protruding beyond the throat. As the styles ultimately come into contact with the anthers, and the latter may still contain pollen, self-pollination may take place. The scales at the throat consist of such low protuberances as to be almost wanting. At night the flower stood fully expanded, white and fragrant. After rain there was much water in the base of the flowers, even among the basal portions of the stamens.

Iceland (Reykjavik; 4. 8. 1886, A. Feddersen). Relative size of parts about as those given above, but the diameter of the corolla 18 mm. Decided protandry. Ultimately the styles protrude 6—7 mm. Various flies and plant-lice were found between the calyx and the corolla.

27. Silene rupestris L.

Norway (Romsdalen, Dovre). ☿: Protandrous in three sets, rather markedly. Calyx about 4—5 mm, petals $4^1/_2$ mm,

corolla 6 mm in diameter, corolla-tube 3—4 mm, the throat is about $1^1/_2$ mm wide, so that entrance is easy for insects with short proboscises.

Switzerland. The corollas are not "meteoric". ☿: Protandry, but styles and stigma develop while the cor.-anth. are shedding their pollen. Possibility of self-pollination (Vaucher; H. M.).

28. Silene acaulis L. (Fig. 44).

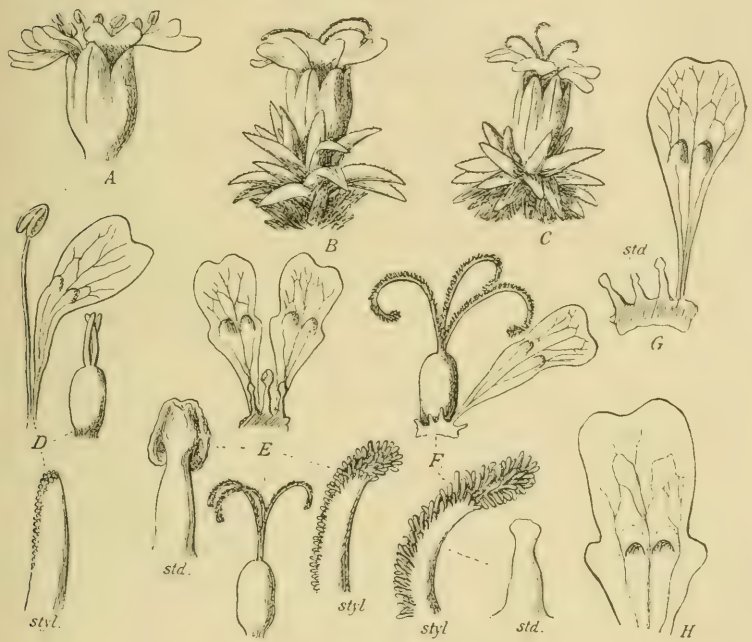

Fig. 44. *Silene acaulis* L.

A—*F*, from Greenland; *G*, from Norway. — *A*, ♂ (about 69° N. lat.); all the anthers open; the parts shown in *D* belong to this. *B*, ♀; *E* belongs to the same form. *C*, ♀ (about 67° N. lat.); *F* belongs to the same form. *D*, from ♂ from Greenland; petal with stamen and pistil $3^1/_2$; *styl*, apex of style. *E*, from ♀ (Upernivik; C. Ryder); the petals and pistils $3^1/_2$, the staminodes (*std.*) $^{37}/_1$. *F*, from ♀ from East Greenland (11. 8. 1888; P. Eberlin); the pistil with the corolla $3^1/_2$; *styl*, style; *std.* sterile stamen. *G*, from ♀ from Tromsö. *H*, Dorsal view of petal, showing the openings into the cavities in the scales at the throat and that petals with lateral projections may occur (compare *G*).

Wherever I saw it, I found the colour to vary; white specimens occurred here and there. Slight perfume in Green-

land. In the Greenland specimens I found flowers formed the year previous to that in which they were to open. In specimens gathered on May 10th, 1887, by Lieut. RYDER, near Upernivik, young flowers, about $^1/_2$ mm in diameter, were found far down among the leaves. (See p. 282, Fig. 24).

Greenland. Trioecism: ☿, ♂ and ♀; as ♀ sets fruit, we have here evidence of insect-pollination. I have not seen ☿ flowers, but LANGE mentions them in "Conspectus Floræ Groenlandiæ" on the authority of VAHL.

♂ are > ♀ (Fig. 44, *A*, *B*, *C*), which is especially seen in the length of the petals and in the diameter of the corolla. In ♂ the petals are 8—10 mm, in ♀ $5^1/_2$—$6^1/_2$, of which the claws are about 4 mm long and the limb scarcely 2 mm (see Fig. *D*, *E*, *F*). The calyx tube is generally larger in ♂ (5—7 mm) than in ♀ (4—5 mm). The corolla-tube in ♂ is 6—$6^1/_2$ mm, in ♀ 4—$5^1/_2$ mm, the diameter of the corolla in ♂ is 7—11 mm, in ♀ 6—8 mm (see Fig. *A*, *B*, *C*). ♂ has always a small pistil with styles $1^1/_2$—2 mm in length, which I have not seen grow and separate (Fig. *D*), as they do in the Alps according to H. MÜLLER. There are shrunken ovules, the integuments of which are however formed. The cal.-st. are the first to develop, then the cor.-st. The styles have at the top some very short stigmatic papillæ, which never grow longer than those shown in Fig. *D*.

♀ flowers have always rudiments of stamens, but in various degrees of development; in some cases they are as much as 2 mm long, and have distinctly marked-off anthers (Fig. *E*, *std*), which are however shrunken, transparent and devoid of pollen; in other cases they have still shorter stamens, and the anthers are hardly indicated (Fig. *F*). Correspondingly with this there appears to be a different degree of development of the size of the flowers, the size of the petals, and the degree of development of the stigmatic papillæ, so that the

flowers which have the larger stamen-rudiments are larger and have shorter stigmatic papillæ, while the flowers which have smaller rudiments are smaller and have longer stigmatic papillæ (compare Fig. *B* and *E* with *C* and *F*); the former are nearer to the hermaphrodite condition, while the latter are more decidedly female. About $^3/_4$ of the style is covered with papillæ. The pistil is 4—6 mm long, the styles about 3 mm, and the ovary 2—$3^1/_2$ mm; consequently, there is no great difference between the size of the ovary in the ♂ flower and ♀, as Fig. *D*, *E*, *F* also shows.

Ripe fruit is set in Greenland; in the capsules investigated I have however found many aborted ovules besides the ripe seeds, of which there were often only 2—4 in each capsule. This is indicative of defective pollination.

Spitzbergen. Dioecism. The ♂ flowers agree with those from Greenland. Petals 10 mm and cal.-st. 8 mm. Aurivillus is of opinion that the passage to the honey is shorter in Spitzbergen flowers than in those from southern countries; this I regard however as doubtful.

Iceland (North coast; St. Stefánsson). Monoecism, dioecism, andromonoecism. ☿ protandrous; the corolla-tube short, 3—4 mm; ♀: the tips of the styles protrude before the flower opens. Petals as much as 7 mm, corolla-tube 5 mm. Sterile stamens as much as $4^1/_2$ mm, pistil 8 mm, of which the styles occupy 3—4 mm; consequently, unusually large female flowers. Stefánsson has gathered flowers from the same place, which are ♀, but approach closely to ☿: the anthers are transparent and without fibrous cells; the cal.-stamens are altogether 8 mm long; the pistil is 5 mm, and the styles are somewhat shorter than in ♀.

Norway, Sweden. (I have examined specimens from Finmark, Nordland, Dovre, Tronfjæld, Åreskutan and Jemteland). Trioecism, but ♂ and ♀ have been found on the

same individual (trioecism and monoecism: Axell). ☿: the stigmatic papillæ were larger than in ♂. According to LINDMAN the high degree of protandry makes self-pollination impossible. ♀: There are two sizes of ♀ flowers (corolla 5—11 mm in diameter) according to LINDMAN. From Tromsö I have seen specimens with corolla-tube 5 mm, staminodes 1 mm, ovary 3 mm in length and corolla 7—9 mm in diameter. From Dovre with diameter $5^1/_2$—7, corolla-tube 5—6 mm, petals 9 mm, calyx-tube 5 mm; the pistil altogether $8^1/_2$—9 mm; the rudiments of the stamens $2^1/_2$ mm. Even before the flower has opened the styles protrude. ♂: like those from Greenland. Ovules rudimentary. Corolla 8—9 mm in diameter, on Dovre even 12 mm, indeed a few as much as 15 mm, calyx-tube $6^1/_2$—8 mm. The pistil-rudiment may attain a length of $3^1/_2$ mm, petals 14 mm, and the corolla-tube 7 mm. Near Hammersfest and Tromsö I saw many ripe fruits in the female plants; on the Skaadavara mountain in Altenfjord, on the other hand, they had remained barren.

The Alps (Vaucher, Koch and H. M.). Trioecism, monoecism. The ☿ flower is as a rule larger than the ♂, which is larger than the ♀. Marked protandry, self-pollination is possible in the case of the ☿ flower (H. M.). Butterfly pollination. ☿ is found only singly, here and there, but appears nevertheless to be of far more common occurrence than in the North.

29. Dianthus superbus L.

This large-flowered species with fragrant, finely divided petals seems to occur with ☿, ♀ and ♂ flowers. According to VAUCHER the flowers open in the evening and close irregularly during the warm hours of the day.

Denmark. ☿: Protandry. ♀ (?): the form *micropetalus* Lge. is probably a female plant.

Kola (specimens from Dr. Brotherus). At the transition-point between the limb and the claw there are long unicellu-

lar hairs with undulating walls and filled with sap. The corolla-tube is about 2 cm in length. ☿ and ♀ occur, or at any rate forms which approach much to ♀; their stamens reach only to the upper part of the ovary; the anthers are about $1^1/_2$—2 mm long and well-developed, but the pollen contained in them is evidently useless, shrunken, etc. A fly was found in one flower.

Germany. Sprengel figures it; gynodioecism; self-pollination impossible. ☿ > ♀. — The Alps. Gynodioecism, androdioecism (?; Vaucher); butterfly-pollination with large flowers in plains and small ones on mountains. ☿: corolla 50—60 mm in diameter, tube 20—25 mm. Marked protandry with movements of stamens. Self-pollination impossible (Vaucher; H. M.).

♀: It does not appear to be a constant feature for the ♀ flowers to be smaller than the ☿; H. Müller, however, records the diameter as 36—45 mm; they are many times rarer than ☿. Rudiments of stamens occur; useless pollen may be present. ♂: Vaucher writes that "les stigmates souvent avortent".

General remarks concerning the Biology of the Flower.

The Form and Venation of the Petals. A single vein enters the petal at its base, and immediately divides into three branches (cf. the foliage-leaves), which may themselves branch, becoming reticulate in large petals (*Sileneæ*); (Figs. 13, 21, 23).

The Appendages of the throat (ligules). In the *Sileneæ* they are in some cases solid, and in others hollow as in the *Borogineæ*.

The Growth of the Petals. The petals often grow during the expansion of the flowers, — this is at all events frequently the case in the *Alsineæ*, — therefore, conclusions with regard to the occurrence of large-flowered or small-flowered types, should be formed with great caution.

Secretion of Honey. Honey is secreted in all the Caryophyllaceae; in the *Alsineæ* it is from the gland-like,

swollen, yellowish base of the calyx-stamens; it accumulates in the sometimes hollow base of the sepals (*Spergularia* and the *Paronychieæ* deviate from this rule). In the *Sileneæ* honey is secreted by the inside of the ring which unites the bases of the stamens and the petals, perhaps also at the base of the ovary. In the female flowers, also, the size of the nectaries is essentially unaltered, even when the anthers are considerably reduced.

The Anthers in the *Alsineæ* are often twisted in such a way that the pollen-covered surface is turned upwards or even outwards, in correlation with the fact that the honey occurs between the petals and the stamens (see H. MÜLLER and A. SCHULTZ). In self-pollinating individuals this feature will hardly be found.

The Styles are, for a longer or shorter distance, covered with stigmatic papillæ, varying in length, being longest in the large-flowered *Sileneæ*. I have, however, never found germinating pollen far down, near the base of the style; but whether this is because the papillæ occurring there, are not functional, I do not know. In *Cerastium trigynum* the styles are very broad towards the apex, even sometimes bi-lobed. In older flowers they are twisted spirally. either to the right or the left, most markedly in the *Sileneæ*. VAUCHER has already explained this as being suitable to the purpose: "afin de recevoir plus facilement le pollen des fleurs mâles."

The Development of the Flowers after Expansion. Protandry is very common in the Arctic Caryophyllaceæ, and the movements of the stamens are the same as elsewhere: first the calyx-stamens stretch out, and bend inwards towards the middle of the flower, then the corolla-stamens perform the same movements, and lastly the styles ripen and spread out; sooner or later however homogamy ensues in almost all the species, and the flower may be entirely

homogamous from the beginning. Protogyny is very rare (*Melandrium apetalum*, *M. triflorum* and *M. affine*, *Cerastium trigynum*, and according to Lindman *Stellaria Frieseana* var. *alpestris*).

Abortion. When the stamens are aborted in a protandrous flower, the corolla-stamens are the first to be reduced, and they are also always even smaller and younger than the calyx-stamens. In protogynous flowers the order of development is reversed.

Everywhere did I find confirmation of the rule established by H. Müller, viz., that protandry or, on the whole, the degree of dichogamy, is correlated with the size of the flower. The larger the flower is, the more pronounced is the protandry, provided the conditions are otherwise similar. In the foregoing I have arranged the species belonging to each genus in the order of the decreasing size of the flower, beginning with the largest-flowered. An examination of some of the genera will prove the correctness of Müller's rule — of course with exceptions, for there should be laid stress on the fact that the external conditions must be similar.

Some species are homogamous almost from the beginning; these are either Arctic or Alpine, or else autumn and winter flowers, or they are very small-flowered. In the *Paronychieæ* pure homogamy seems to be frequent. These facts appear to me to be connected with the fact that the Arctic-Alpine and the small flowers are probably not so quickly developed as in southern countries, or as are the large flowers. It is above all in the physical conditions that we must look for the explanation of these differences in the development.

Self-pollination is by no means rare; it appears to be least common in some of the large-flowered *Sileneæ*, for instance *Dianthus superbus*; the vigorous development of the corolla is there followed by a quicker development of the

stamens. But in many homogamous or slightly dichogamous and small-flowered species, self-pollination is a process which regularly takes place, and which produces an excellent result. It is seen here, as in the Greenland *Cruciferæ*, *Saxifragæ*, etc., that fruit-setting follows immediately after flowering, and that there is a gradual succession of the sizes of the fruits, according to the age of the flowers.

Polygamy (Pleogamy). Many of the High Arctic, and even small-flowered and homogamous species have polygamy, especially gynodiœcism (for instance *Cerastium alpinum*, *C. trigynum*, *Stellaria longipes*, *S. borealis*, *Minuartia biflora*, and others, even Arctic species of *Melandrium*). Polygamy must be regarded as an unfavourable feature where the country is as poor in insects as are the Arctic countries.

From the preceding detailed descriptions it is evident that few species have hermaphrodite flowers only, and continued investigations will probably result in the reduction of even their number; also probably many more combinations of ☿, ♀ and ♂, than are now known, will be found.

A peculiarity common to the gynodiœcious species is the varying degree of reduction of the stamens in the female flowers; many examples of this have been mentioned and figured above. There is every possible degree of reduction of the anthers, according as the development which has once begun, stops earlier or later; I have seen no female flower which was entirely without rudiments of stamens. To this must be added those hermaphrodite flowers in which a few or several stamens are abortive. Several successive stages of more or less decided abortion may thus be demonstrated, and that often in one and the same species.

Another peculiarity which accompanies the one mentioned above, is that the corolla is diminished in size more or less in all the female flowers. There are extremely few

Caryophyllaceæ of which the female flowers are similar to the hermaphrodite flowers in size, as they are in *Minuartia biflora.*

The alterations in the structure of the flowers in individuals of the same species, of which so many examples have been given in the foregoing, will be understood, to a certain extent, if the ontogeny of the flower is known. Those organs which have developed first, or at an early stage, grow most quickly and vigorously in the flower (especially the calyx and pistil and the calyx-stamens), and will have the best chance of becoming developed, should any check occur; while the last-developed or slow-growing organs may become dwarfed, or are even completely suppressed — all according to the point of time when the check occurred. In the protandrous flowers it is the corolla-stamens which are suppressed whenever the androecium is reduced, which is in perfect harmony with the ontogeny. In the protogynous flowers the pistils hasten as usual, and attain full maturity before the stamens, and so, if the check occurs very early, a purely female flower may be produced.

The size of the flowers evidently has also a certain connection with the longevity of the individual: annual species generally have smaller flowers than perennials; this is also confirmed with regard to the Caryophyllaceæ as a whole. Further, the numbers in the flowers are dependent on the size of the flowers. But the causal conditions are still problematic in many respects, viz., with regard to the dependency of the form of the flower on the prevailing conditions, especially those relating to nutrition. Dichogamy or pleogamy in the Caryophyllaceæ must, as a whole, be regarded rather as a sign of weakened constitution, or of unfavourable conditions of life, than as an advantage.

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14.

Liliales.

By

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1920.

Of the order **Liliales** several species, belonging to different families, advance to the arctic limit of forest occasionally even crossing it, not attaining, however, a wider distribution in the arctic territory where they do not belong. We find also that they in the alpine regions do not, or only occasionally, cross the limit of forest, cf. remarks in SCHROETER: Pflanzenleben p. 354—5.

The principal of those species are the following:

1) **Veratrum album** L. and the closely related **V. viride** Ait. extend respectively in the river-valleys of Northern Eurasia and Northern America to the coasts of the Arctic sea.

2) **Streptopus amplexifolius** (L.) D. C. is an E. Asiatic —N. American forest plant; the fruit is a berry, and it has probably, through the agency of birds, been brought to the subarctic copses of the southernmost part of Greenland.

3) **Lloydia serotina** (L.) Sweet — closely related to *Gagea* — advances on both sides of Bering's strait farther into arctic territory than any of the others. Thus it is found at Cape Lisburn and extends even as far as the purely arctic New Siberian Islands.

4) **Allium schoenoprasum** L. (including **A. sibiricum** L.) is found in the island of Kolgujew, in the river-valleys of N. Asia up to the Arctic sea, and on the north coast of Alaska.

5) **Iris sibirica** L. (and related species?) extend to the coast on both sides of Bering's strait.

As to the structure and biology of the majority of the above-mentioned species the reader is referred to KIRCHNER, LOEW & SCHROETER's: "Lebensgeschichte" where — on Alpine material — these questions have recently been treated.

Widely distributed in the arctic territory are only the two following species of the genus

Tofieldia:

1) **T. palustris** HUDS., circumpolar, common from the subarctic territory far into the arctic, probably without reaching the purely high-arctic regions, however.

2) **T. coccinea** RICH., N. Asiatic, N. American, found besides in the northernmost two-thirds of Greenland, everywhere rare or perhaps overlooked; numerous of its Asiatic occurrences are only known from previous erroneous determinations, corrected by OSTENFELD (Fl. Arctica p. 32).

A third species: *T. calyculata* WAHLENB. is distributed throughout nearly all the mountain regions of Central Europe, whence it often descends into the lowland, whilst it only in a few places crosses the Alpine limit of forest: the variety *glacialis* REICHENB.

The structure and biology of *T. calyculata* is extremely well-known, and the same applies partly to *T. palustris*. An account of this, based upon Alpine material, is found in LOEW & KIRCHNER's: "Lebensgeschichte" p. 229 ff., a copious literature being quoted here, too. Cp. also the description of the closely related *Narthecium ossifragum* HUDS. ibid. p. 244 ff., and RAUNKIÆR p. 138 ff. The following observations,

having all been carried out upon arctic, living and alcohol material, chiefly from Greenland, will therefore serve mostly as a complement, especially with regard to the least known of the species: *T. coccinea.*

Occurrence in nature. *Tofieldia palustris* and *T. coccinea* grow on moist spots among heath- and bog vegetation, more rarely on fresh plantless moraines. They occur most frequently here as firm cushions or cakes which are held together by the vigorous secondary roots (Fig. 1, *A*). They attain their highest development when growing among bog-mosses. Here the leaves become longest, and the floral shoot tallest, but on the other hand, the stalks are able to creep better and more widely, and consequently we do not get here as large and firm cakes as otherwise. The habitats are covered by snow during winter.

The shoots are short-jointed, flat, frequently erect, more rarely, through want of space, obliquely ascending and, in vigorous specimens, each shoot bears from 6—8 leaves. During several years the shoot remains on a purely vegetative stage until finally ending in an inflorescence. Some of them remain on the vegetative stage. Structure of shoot cp. Fig. 1, *A—D.*

The leaves are all uniform, apart from a slight difference in length, the lowermost being the smallest, evergreen, two-rowed ensiform, equitant with a long sheath. Below the green leaves some withered ones (often black-spotted by fungi) are found, and at the base setaceous, vascular strands are seated originating from older marcescent leaves. Scale-leaves are not found. The lateral shoots are formed in the uppermost axils of the leaves, normally only one or two are developed.

Fig. 1.

A, *B*, *C*. Structure of shoot in *T. palustris* (Finse, Norway).

A. Habit drawing of two flowering shoots which only cohere by the aid of the roots. *b*, the scape with its sheath-formed bract.

B. The main-shoot, *I*, has two withered leaves (*1*—*2*) and six fresh (*3*—*8*). In the axil of *2* a shoot: II, is to be seen, and in the axil of *3* another one *II*, of which 4 leaves are visible. Magnified, detailed drawing of it in the following (*C*).

C. Shoot with its subtending leaf: *f*, and with 3 leaves marked *1*, *2*, *3*, *4*. *1* and *2* turn their back to the mother-axis.

D. *T. coccinea*. Foliage shoot with withered remains of leaves, from unfavourable habitat. (Dove Bay, E. Greenland; leg. A. Lundager, 27. 6. 1908).

E. Germination in *T. calyculata*. (Drawn by E. W.)

In *T. coccinea* there is as a rule 9(—11) vascular bundles (Fig. 2), in *T. palustris* 11(—13). In the first-mentioned the leaves are often more flaccid (Fig. 1, *D*), frequently partly decumbent, especially in exposed places, whilst they, in the latter, always are rigidly erect.

The structure of the leaf is in all essentials identical in the two species. The sheath is constructed like a normal leaf, above this the leaf is isolateral, has an equal right and left side, an upper and lower margin (Fig. 3). The epidermis consists, except on the upper (inner-) side of the sheath, of rather small cells, the walls of which are slightly undulating, highly thickened, porous and covered by a well-developed cuticle which also spreads to the guard-cells of the stomata (Fig. 3 *B*, *D*). The stomata are arranged longitudinally, their slit is quite diminutive, the intercellular cavity beneath them is quite small. The base of the sheath consists of hyaline parenchyma; a little higher up, on the morphological lower side, we find the chlorophyll tissue consisting of several layers of cells, whilst the upper side is constantly non-chlorophyllose. Above the sheath the chlorophyll tissue is homogeneously developed on both sides, the non-chlorophyllose part occupying the centre of the leaf, extending right to the tip of the leaf (Fig. 2, 3, *A*, *B*). In contradistinction to *Narthecium* (vide Raunkiær) no air-chambers are found in the chlorophyll layer on transverse sections.

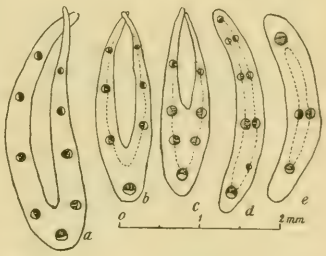

Fig. 2. *T. coccinea*. Nordre Strömfjord, Greenland. *a*—*e* show sections in various height through a foliage leaf. The xylem of the vascular bundles is dark. The dotted line shows the boundary between the chlorophyll tissue and the aqueous tissue; *a*, showing the basal part of the sheath, has no chlorophyll. (Drawn by M. P. P.)

The cells in the chlorophyll tissue are parallelepipedic and frequently no intercellular spaces are seen in transverse sections; in longitudinal sections, however, quite small ones are to be seen. The cells of the chlorophyll tissue contain chlorophyll grains filled with starch. In the isolateral part the vascular bundles approach by twos to each other, and the uppermost one is entirely connated of two (Fig. 2 *e*, 3 *A*). In transverse sections the large, crescent-shaped coverings of bast are to be seen.

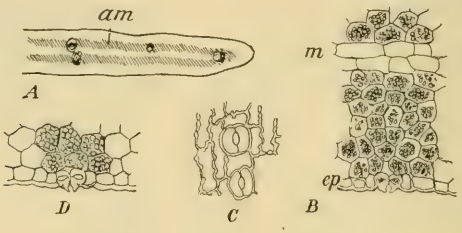

Fig. 3. Anatomy of leaf.

A, *B*, *C*. *T. palustris*; from Jakobshavn, W. Greenland.

A. Transverse section of a foliage leaf above the equitant part. The hatched *am* is the chlorophyll tissue; the epidermis and the central aqueous tissue are light.

B. A part of the same section, more highly magnified; *ep*. Epidermis with thick cuticle and a stoma with very minute air cavity. Chlorophyll tissue almost without any intercellular spaces, the cells filled with starch; *m* aqueous tissue.

C. Epidermis with two stomata, longitudinally placed. The walls of the cells are highly thickened, slightly undulating.

D. Transverse section of a leaf of *T. coccinea* (Danmarks Ø, E. Greenland leg. N. Hartz). (Drawn by E. W.)

The scape of inflorescence is as a rule leaf-less, yet in vigorous specimens 1—2 leaves may be found, the uppermost one at least having the character of a bract (Fig. 1). In *T. coccinea* 2—3 stem-leaves are nearly always present (Fig. 4 *A*), the uppermost one having, in this case, less of the character of a bract.

The inflorescence in *T. palustris* is nearly always a globular head (Fig. 1 *A*), more rarely a subcylindric spike. In *T. coccinea* the elongated spike is the normal form, the globular the rarer one (Fig. 4 *A*, *B*), but it varies according to the quality of the habitat. In *T. coccinea*, moreover,

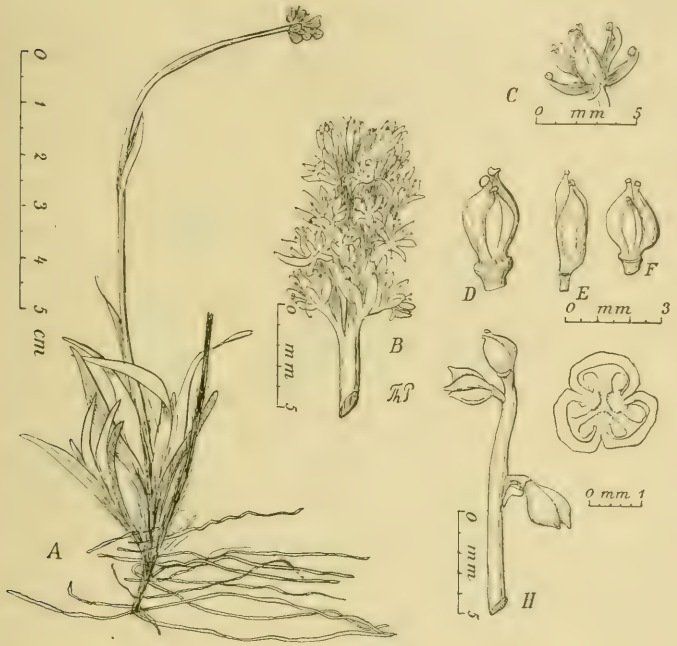

Fig. 4. *T. coccinea.* Nordre Strömfjord, Greenland.

A. Habit-drawing of a weakly flowering specimen growing in *Sphagnum*.
B. Inflorescence of a more richly flowering specimen.
C. Single flower, shortly before the hermaphrodite stage.
D, *E*, *F.* Almost ripe fruits in various positions; *D* and *E* the same specimen; note the asymmetry.
G. Transverse section of the ovary.
H. Uppermost part of the inflorescence, showing the downwards-directed carpotropic curvature, characteristic of the species. (Drawn by Thorbjorn Porsild).

single isolated flowers are frequently to be found below the spike, just as in *T. calyculata* and in other species of the genus.

The flowering season is the middle of the summer, consequently the species do not belong to the earliest flowering. In an average year they will, on the latitude of Disko, be out from the end of July, and then flowering specimens are to be met with all through the rest of the summer, because the floral shoots from the same tuft are not all of them developed simultaneously.

Under each flower a small 3-dentated bractlet is present which often envelops the peduncle. In *T. palustris*

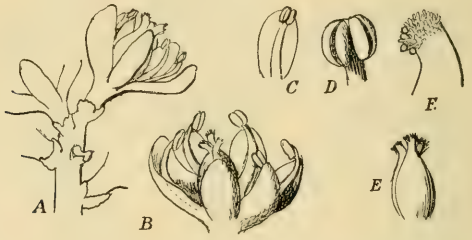

Fig. 5. *T. palustris* (Norway.)

A. Part of inflorescence; note the small, 3-dentated bractlet.
B. Flower at the beginning of the hermaphrodite stage: the stamens arise from the spoon-formed perigonial leaves.
C. Stamen in a perigonal leaf when the flower bursts.
D. Anther with open valves.
E. Carpels in the stage of pollination.
F. A single carpel, more highly magnified, showing pollen-grains on the stigma. (Drawn by E.W.)

it is always shorter than the peduncle (Fig. 5 *A*), in *T. coccinea* just as long as this or longer (ABROMEIT). In the latter a fairly well-developed "calyculus" is as a rule present, a bi-symmetrical whorl of 3 small leaf-formations of which one is turned outwards, the other two transversal (Fig. 6). The morphological interpretation is uncertain. In *T. palustris* it is normally absent, but may also, according to ABROMEIT, occur occasionally.

Diagram. EICHLER's diagram of *T. calyculata* shows, besides the zygomorphy in the calyculus, a slight irregularity in the mutual size of the carpels. This also applies to the arctic species, especially to *T. coccinea* (Fig. 6), where it appears to be even more strongly developed than in EICHLER's diagram. This difference is undoubtedly connected with the carpotropic movements (see below).

In *T. palustris* the perianth is purely white, or with a greenish rather than a yellowish tinge, in *T. coccinea* it is purely white on the inner side, deep purplish on the exterior, especially along the median line of the leaves. Also the upper part of the scape and the carpels are of a beautiful purple-red colour. This bi-colouring is in live specimens very conspicuous, and when the species grow together they are easily distinguished from each other by the colour of the flowers alone. But in herbariums the red pigment often disappears entirely, the flowers in both species becoming yellowish, hence the numerous confoundings and erroneous determinations.

Fig. 6. Floral diagram of *T. coccinea*. Note the asymmetry in the carpets. (Drawn by M. P. P.)

The biology of the flowers (Fig. 5 *B*—*E*, 4 *C*) has been studied by H. MÜLLER in the Alps on *T. calyculata* which he found proterogynous, while *T. palustris* was almost homogamous. In spite of a greater abundance of honey-secretion in the latter he found a greater number of insects visiting the former. Greenlandic flowers of *T. palustris* and *T. coccinea* were almost homogamous with a slight indication of proterogyny. Visiting insects I have never seen there. In *T. palustris* MÜLLER draws the stamens as freely projecting in the flower, in Greenlandic living material the filaments were curved downwards into the cavity of the perigonial

leaf (Fig. 5 *B*, *b*, 4 *C*), this was especially prominent in the case of *T. coccinea.* During calm weather the cavity of the perigonial leaf is filled with pollen. When the flower has been open for some time the filaments, as well as the perigonial leaves, start curving upwards, and then the introrse anthera cannot avoid touching the stigmas. Thus cross-pollination is possible, but self-pollination the rule.

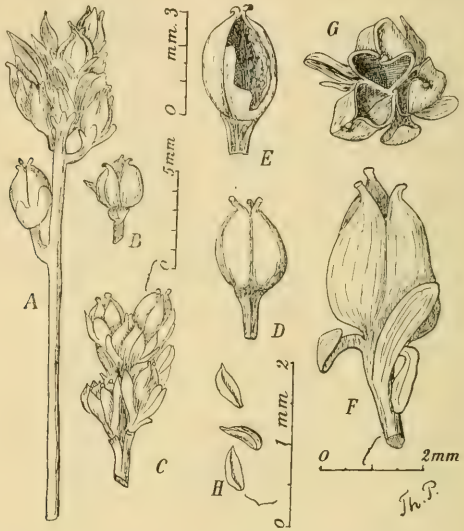

Fig. 7. *T. palustris* (Disko, Greenland).

A. Hibernated inflorescence with upwards-directed capsules, characteristic of the species.

B. Single, complete fruit of the same.

C. Almost ripe inflorescence gathered late in autumn.

D. Fruit, almost ripe, but not yet open. (The perigonial leaves removed). Note the almost perfect symmetry, as against *T. coccinea.*

E. Hibernated capsule with walls partly fallen off, typical for the species. Some seeds are still seated on the placentas.

F and *G.* A "normally" opened fruit (a rare case in the species). *F.* in moist condition. *G.* dry, seen from above.

H. Seeds. (Drawn by T. P.)

After the pollination the inflorescence, which hitherto has been slightly nodding, straightens itself up, and the

scape becomes rigid. The head or spike is stretched a little (Fig. 7 *A*). The perigone withers, but persists for a long time round the carpels (Fig. 7 *C*). In *T. palustris* the capsule is ovate, often a little brownish in colour and bent upwards (as in *T. calyculata*) (Fig. 7 *A*, *C*), whilst it in *T. coccinea* is shorter, subglobose and bent downwards (Fig. 4 *H*). The lowest fruits in the inflorescence bend right downwards parallel with the scape, the uppermost obliquely downwards or the top one only horizontally. This carpotropic movement begins immediately and is continued during the ripening of the fruit.

The ripening of the fruit is very late. Even on Disko, that lies far to the south of the Polar limit of the species, it is very difficult, even after favourable summers to find ripe fruits in the autumn, and if the unripe fruits are brought home the ripening is not continued. Exceptionally I have, however, found single, quite ripe fruits of *T. palustris* late in the autumn; the dehiscing is septicidal, forming a slight opening so that the seeds might be shaken out (Fig. 7 *G*). I have had no chance of seeing *T. coccinea* late in autumn. The majority of fruits in *T. palustris*, and probably also in the other, do not thus attain to ripen their fruits before the snow comes. Consequently the ripening must take place under the snow. I have looked through a large material of hibernated fruits of both species and only succeeded in finding a single "normally" opened fruit. Instead, the very thin capsule-walls had gone to pieces, and the seeds had got out through the holes which had come into existence in that way. Often the capsules may be quite "skeletonized" so that only the backs of the carpels are left (Fig. 7 *E*).

Sernander („Spridningsbiologi" pag. 354) has gathered *T. palustris* with seeds in the capsules in spring at the time when the snow was beginning to melt, and he therefore includes

them among the winter-standers. To a certain extent this is right, as it does not attain to ripen its fruits till the snow comes, and consequently may happen to spread its seeds on the snow. But the white, paper-thin capsules of *Tofielda* are to a less extent adapted to this than for instance, the *Luzula* species, the brown capsules of which are saturated with a substance which makes them proof against the various attacks of the first winter and preserves their hygroscopicity.

What brings about the skeletonizing of the *Tofieldia* capsules, I do not know. If it had been effected by mechanical wear of drifting snow in the spring-time there would always be found some which had been lying in sheltered places and remained intact. The apertures are irregular, as if the thin parchment-like capsular membranes had, through iterated freezing or exsiccation, become so fragile that even the slightest touch was enough to cause the apertures.

The production of seeds is no doubt abundant in both species, judging by the number of well-developed ovules and by the occurrence of the species in nature. Vegetative propagation is practically excluded, because even the strongest stream issuing from melting snow would hardly be able to break asunder the cakes which are made up of the strong roots felted together. Only in loose growing mosses a liberation of the lateral shoots takes place when the rhizome dies away at the back.

The seeds (Fig. 7 *H*) in *T. palustris* are small, yellow, a little triangular and slightly curved, with few wrinkles faintly marked on the testa. They weigh 0.03 mg. In *T. coccinea*, of which I have gathered but a few seeds in hibernated capsules, they were of about the same size and appearance.

Germination. The first stages have been seen by KLEBS (quoted in "Lebensgeschichte") and later on by WAR-

MING in *T. calyculata* (Fig. 1 *E*). After having emerged from the testa the cotyledon is geniculate bent, and at a very early stage a whorl of roothairs is produced at the base of the young root. The later stages are not known, but they might agree with those in *Narthecium* described by BUCHENAU.

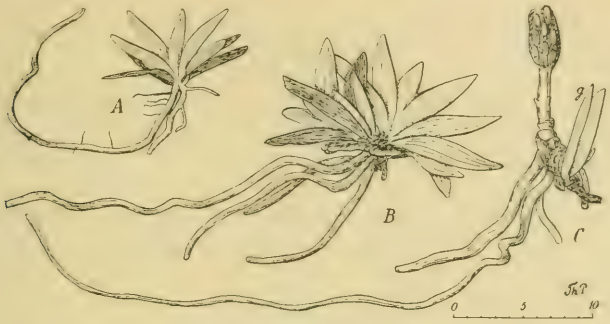

Fig. 8.

A. Seedling of *T. palustris* at the end of the second period of vegetation.
B. 3—4 years old seedling of the same species. Both from Disko, Greenland.
C. Retarded inflorescence, extricated from an almost withered specimen of *T. coccinea*; g. small vegetative lateral shoot. Nordre Strömfjord, Greenland. (Drawn by Th. P.)

Seedlings (Fig. 8) are easily found in nature, but it is very difficult to find the very first stages because they are so small. The earliest formed foliage leaves wither rapidly, and the young plants pass through a period of strengthening, which lasts for many years, before they attain to flowering.

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Besides, I have made freely use of notes and drawings by Professor E. Warming.

15.

Scrophulariaceae.

By

Fr. J. Mathiesen.

1921.

Preface.

In the present paper, partly on the basis of notes on the subject found in previous publications, and partly on the basis of my own investigations, I have given a description of the ramification, shoot-structure, flower-biology and anatomy of some Arctic and Subarctic Scrophulariaceae; in addition to which, under each species, the geographical distribution has been briefly mentioned, and, as far as the literature on the subject rendered it possible, the nature of the habitat.

Besides the herbarium and alcohol material belonging to the Botanical Museum of the University of Copenhagen, I have, through the courtesy of Mrs. Thekla Resvoll, Dr. phil., with respect to several of the species, had an opportunity of investigating some excellently preserved material, collected on the mountains of Norway.

The subject-matter of the present paper was worked out in the Plant-anatomical Laboratory of the University of Copenhagen, and I wish to express my grateful and heartfelt thanks to the Director, Professor C. Raunkiær, for his advice and help during the work.

The majority of the figures illustrating the structure of the flowers, are drawn by Professor Warming, to whom also my most sincere thanks are due, partly on account of the interest he has taken in my work, and partly because he so

generously placed his notes on the Arctic Scrophulariaceae at my disposal. Fig. 20, *B*, *C* and *D*, Fig. 40 and Fig. 44, which are published here for the first time, have been redrawn after Professor Warming's originals, in order to be reproduced according to the method employed here. The remainder of the figures are drawn by myself.

Mr. M. Porsild, mag. sc., Director of the Danish Arctic Station, Greenland, has very kindly read through great parts of my manuscript, and made several additions of a biological nature, besides having also kindly permitted me to use his notes on the geographical distribution of Arctic plants. For the help thus rendered to me I herewith beg him to accept my best thanks.

The following species have been investigated:—

Veronica fruticans Crantz.
— *alpina* L.
— *officinalis* L. f. *glabrata* Fristedt.
Castilleia pallida (L.) Kunth.
Euphrasia arctica Lange.
Bartschia alpina L.
Pedicularis lapponica L.
— *sudetica* Willd.
— *euphrasioides* Steph.
— *Sceptrum carolinum* L.
— *capitata* Adams.
— *hirsuta* L.
— *lanata* (Willd.) Cham. & Schlecht.
— *flammea* L.
— *Oederi* Vahl.

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Veronica fruticans Crantz (*V. saxatilis* Scop.).

Alcohol-material from Greenland (Julianehaab, leg. Lützen, 3. 7. 1887; Præstefjældet, leg. E. Warming, 2. 8. and 6. 8. 1884) and Northern Norway (Kåfjord, leg. E. Warming, 15. 7. 1885). — Herbarium-material from Greenland, Iceland, the Færöes and Fennoscandia.

Lit.: Axell, 1869, p. 102; Lange, 1880, p. 73; 1887, p. 261; Müller, 1881, p. 267; Warming, 1888, pp. 35, 75 and 87; 1890, p. 203; Rosenvinge, 1892, p. 685; 1896 (II), pp. 128, 144, 161; Wagner, 1892, pp. 8 and 21; Hartz, 1894, pp. 9 and 57; 1895 (I), pp. 273, 289; 1895 (II), p. 335; Hartz and Kruuse, 1911, pp. 352, 357, 359 and 409; Koch, 1895, p. 117 et seq. and p. 127; Norman, 1895, p. 452; Knuth, 1899, p. 167; Porsild, 1902, p. 230; 1920, p. 141; Huchedé, 1907, p. 72, fig. IV, B^2, fig. V, C^3, and fig. VI, C^5; Sylvén, 1906, p. 80; Kruuse, 1905, p. 175; 1906, p. 248; 1911, in part IV pp. 202, 207, 243, 261 and 262, besides many notes in the preceding parts; Schröter, 1908, pp. 221 and 656.

An evergreen, nanophyllous[1], sympodial under-shrub-chamæphyte which has a main root that dies away early (according to Sylvén), and develops adventitious roots fairly abundantly; the winter-buds are raised at most a few cm above the surface of the ground; older, vigorous specimens form small tufts (Kruuse, 1906, p. 248). The shoot-development extends over two years; during the first year a horizontal or obliquely-ascending part is developed, only a few cm long and furnished with a few (3—7) pairs of foliage-leaves; the next year the shoot

[1] C. Raunkiær: Om Bladstørrelsens Anvendelse i den biologiske Plantegeografi (Bot. Tidsskrift, Kjbh., Bd. 34, 1916).

usually continues its growth in a vertical direction, larger leaves are developed, and the growth can be terminated by a few-flowered raceme without a terminal flower. Special bud-scales do not occur; during the winter-rest the point of the axis is protected by the uppermost, not yet expanded pair of foliage-leaves, which are in contact with each other by their hairy margins. After the fruit has ripened, the stem dies as far down as to somewhat above the boundary line between the 1st and 2nd year's growth; the perennial basal portions bear the innovation shoots. Principal buds proper do not occur, but the uppermost buds appear generally to be the most advanced, and it is evidently especially these buds which produce the flower-bearing axes, while the lower ones often produce only small, weak, few-leaved shoots which — as recorded by Warming (1890, p. 205) and as also shown in Fig. 1 — may be somewhat runner-like and furnished with only a few small leaves. The specimen illustrated in Fig. 1 is rather scantily branched; each of the floral shoots has only two real "innovation-buds", and of their parent-shoots the one to the left has also had two, of which one has developed into a vegetative shoot; the parent-shoot to the right is somewhat more richly equipped: in addition to the lowermost quite small shoot it bears two opposite floral shoots, and in the axils of the next pair of leaves two more shoots, of which the one (cut-off) was floral. Such a difference

Fig. 1. *Veronica fruticans.* (Greenland. Præstefjældet. 2. 8. 1884). (About nat. size.)

between shoots from two opposite leaves, that the one becomes vigorous and floral, and the other vegetative only, is very common; it appears to be the rule that the shoot which turns outwards towards the periphery of the tuft, becomes more vigorous. It happens not rarely, however, that the short, vegetative shoots are later on instrumental in the formation of floral shoots, in that the latter arise as lateral shoots upon them; in such a case the part of the parent-shoot above these lateral shoots dies away, as is the case in the floral shoot. The development of the lateral shoots usually takes place in the second year of the parent-shoot, and consequently simultaneously with the flowering.

The Leaves are rather thick, entire or slightly serrate; on the median rib and along the margin there is a sparse covering of non-glandular hairs; such are also found on the stem and in the floral region, viz., on the calyx and ovary. In the Botanical Garden in Copenhagen the leaves on the new innovation-shoots, developed during the last summer, remain green and fresh during the winter; on the flowering shoots, in my herbarium-material, the leaves from the previous year were withered in some cases; most often, however, they were green.

As a rule, the basal portion of the shoots takes root abundantly, and is drawn down by the roots to the surface of the ground; in the individual illustrated in Fig. 1, which has a somewhat more erect growth than is generally the case, adventitious roots are only scantily produced; the roots are developed at the earliest in the second year of the shoots.

The basal portions of the shoots have growth in thickness and may live several years; an individual from Greenland (Ikalik) had a prostrate stock, 4 mm thick, which showed 16 annual rings.

The Flower-biology has been investigated by H. Mül-

LER (the Alps) and E. WARMING (Greenland and Northern Norway). The flowers are large and conspicuous; also in the Arctic regions, as a rule, they are of a pure and bright colour; but according to M. PORSILD, in northern Greenland a white-flowering variety may commonly occur. The ultimate diameter of the corolla is very constant, being 10—12 mm in material from the different localities; I found it to be particularly large in some material from Iceland, viz. 14 mm (in the Alps, according to Müller, only 6—7 mm). "The corolla-tube and the throat is white, and furnished with a wreath of hairs; then follows a dark, brown or reddish ring and then the deep-blue limb. The corolla-tube is $1^1/_2$—$2^1/_2$ mm in length (according to Müller 3 mm). As in the Alps the filaments taper very much at the base, are about 5 mm in length and, as the pistil is of the same length, the stigma and anthers stand at the same level. The flowers are homogamous. In fully expanded flowers self-pollination appears to be able to take place only with difficulty, as the stamens diverge so much laterally and the anthers are thereby removed from the stigma on the straight outstretched style; but self-pollination might have taken place at an earlier point of time, for I have seen a flower (from Greenland at 67° N. lat., Aug. 6) which, perhaps on account of gloomy and rainy weather, was only slightly expanded and in which the one anther was open, so that the pollen fell out of it down upon the stigma which stood close to it and which appeared to be fully ripe. The ovary is covered with small upwardly directed, adpressed hairs, and the style is 2—3 times longer than the ovary. Ripe fruit is produced in West Greenland at least up to 70° N. lat." (E. WARMING, 1890, p. 203).

V. fruticans is homogamous also according to AXELL and H. MÜLLER. The style, however, appears to me to be always slightly longer than the anthers; the outspread posi-

tion of the latter is distinctly seen in Fig. 5, *C*; the figure is drawn from living material from the Botanical Garden in Copenhagen.

According to M. Porsild, near its northern limit in Greenland it flowers late and even sets fruit; but it is only in favourable, dry autumns, without too much frost, that its seeds ripen. Unripe fruits live through the winter, but perish without developing further. The structure of the shoots explains, as in *V. alpina* (Th. Resvoll), the late flowering. There was, however, ripe fruit to hand from all localities. Kruuse (1906, p. 248) in the Angmagsalik-district notes "abundant ripe fruit".

Geographical Distribution according to Lange: Greenland, the Ural Mountains, Lapland, Finmark, Norway, Iceland, Great Britain, the Alps and the Pyrenees. Besides this it is recorded from the Færöes. Its certainly known north limit in West Greenland is 70°17′ on the continent (Vajgattet), from 70°—67° it occurs in isolated specimens only, and not until further southwards is it common; consequently, in Greenland it belongs to the southern types (M. Porsild). In East Greenland it occurs as far north as the Scoresby-Sound-district (Hartz and Kruuse, 1911).

According to Warming (1888) and Rosenvinge (1896 (II)) in West Greenland the species grows in willow-copses, birch-copses and on "herb-slopes", and in places whence snow melts early it can ascend as high up in the mountains as 750 metres (Lange, 1880: in grass-covered, open places, in rocky clefts). M. Porsild informs me in confirmation of this that its natural habitat is the edge of the willow-copse, there it grows on warm, sunny slopes which are not too dry; the species thrives but badly when overshadowed; it needs snow-covering throughout the winter but must be early freed from snow; at its north limit it

does not at any rate belong to the real snow-flora. In the Scoresby-Sound-district it is found "in particularly well sheltered luxuriant, humid, herby slopes with high snow-cover in winter," but here it is very rare (KRUUSE, 1905, p. 175). In the Angmagsalik district, where it is somewhat more common (KRUUSE, 1906, p. 248), besides growing on the herby-slopes, it is also noted from the "steps of steep rocks above the slopes." According to NORMAN, in Northern Norway the species is found on all kinds of stony substrata rather than on grassy ground, and "it very much prefers the sunny side, especially the side facing directly south, and occurs only very rarely on the indifferent (eastern and western) sides". In the Alps it is recorded from "Schneeblössen" (SCHRÖTER, p. 656), spots where the wind sweeps the snow away in winter time.

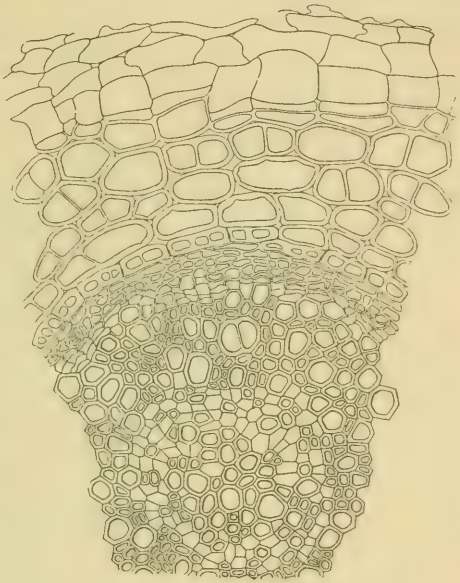

Fig. 2. *Veronica fruticans.* Transverse section of an adventitious root (about $^{230}/_{1}$). (Greenland.)

Anatomy. The Root. The epidermis of the adventitious roots dies away early; the outermost layer of the cortex is developed as an exodermis with cuticularised walls. Even before any secondary growth has taken place in the stele, a cork-cambium is developed in the layer under the exodermis, which is instrumental in the formation of a few-

layered cork (cf. Fig. 2). The walls of the primary cortex attain a rather considerable thickness; this is especially the case as regards the endodermis; both in this and in the

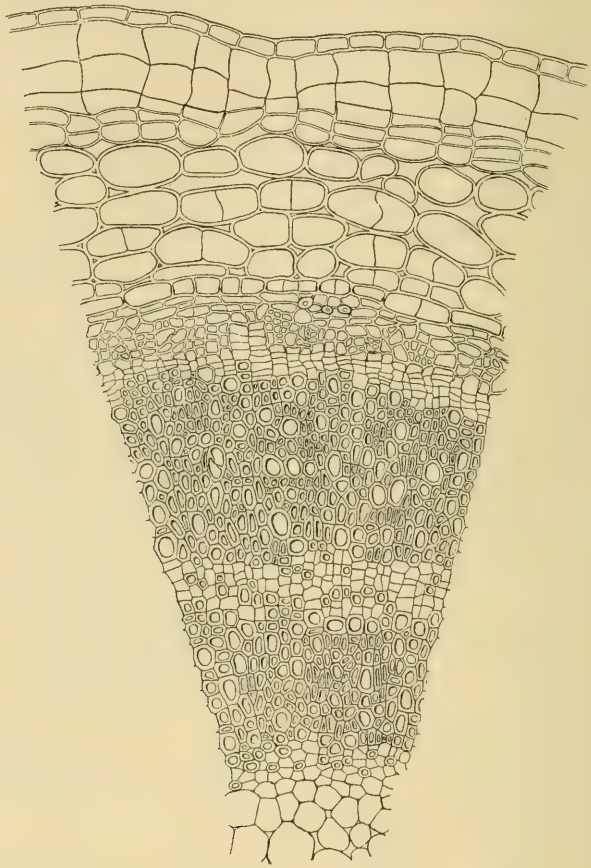

Fig. 3. *Veronica fruticans.*
Transverse section of the stem (about $^{200}/_{1}$). (Greenland.)

other layers, radial walls are formed during the secondary growth of the root.

In the wood of the 2-year-old root illustrated in Fig. 2, an annual ring is formed outside the central part which was developed during the first year; the limit between them is

easily discernable, since they are separated by a zone in which the vessels and wood-fibres are intermixed with non-lignified, axially elongated parenchymatous elements.

The Stem. In the lower persistent parts of the stems, a cork-cambium commences activity during their second year; it appears in the outermost layer of the cortex and forms a few-layered cork (Fig. 3). The cells of the primary cortex are rather thick-walled and show division by radial walls; they contain chlorophyll-grains. The endodermis has very distinct Casparian dots (as in the root). In the pericycle small groups of hard-bast cells are found. The figure shows a portion of the transverse section of a stem with apparently two growth-rings; between the two rings consisting of vessels and wood-fibres there is a zone intermixed with thin-walled and non-lignified cells; however, in reality the stem is 3 years old; during the first year only the innermost zone of the xylem with the small scattered vessels being developed. According to whether the shoots during the first year succeed in becoming more or less vigorous, so also does the thickness of the xylem of the first year vary; shoots may sometimes be found in which a continuous wood-ring has been developed as in the following years.

In the upper part of the shoot which dies away, no cork-formation takes place, the cortical cells are less thick-walled than in the lower part and richer in chlorophyll and Casparian dots are less distinctly developed. Hard bast is wanting or is scantily present in the pericycle, and the wood-ring is quite narrow. From all the axial organs medullary rays are quite absent.

The Anatomy of the Leaf has been investigated by Koch and Huchedé; my investigations entirely bear out the conclusions arrived at by them. The epidermal cells of

both the upper and lower surface have undulating lateral walls, those of the epidermal cells of the lower surface are however more strongly undulating; under a higher magni-

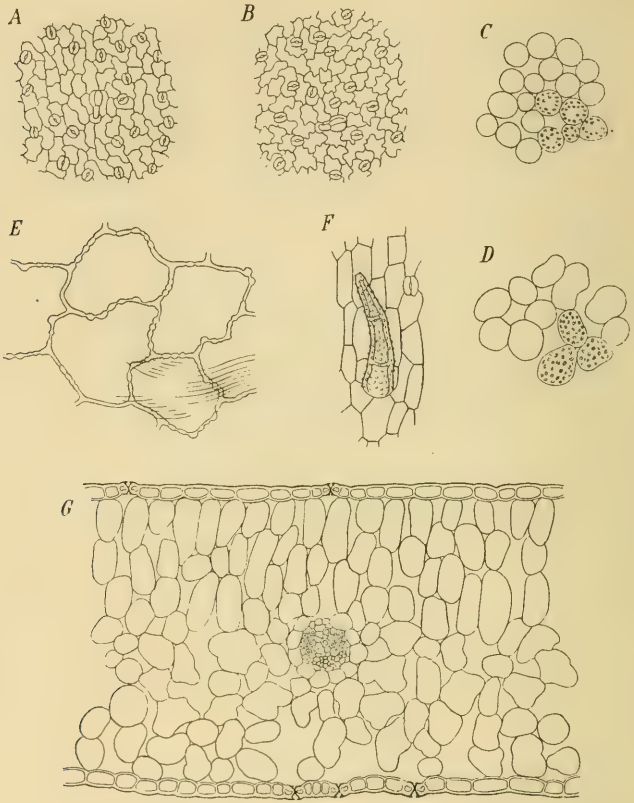

Fig. 4. *Veronica fruticans.*
A, Epidermis of the upper, and *B* of the lower surface of the leaf. *C* and *D*, The uppermost and lowermost layer of the mesophyll respectively, shown in surface view. *E*, Epidermal cells from the upper surface of the leaf, more highly magnified. *F*, A non-glandular hair from the mid-rib. *G*, Transverse section of the leaf (*A* and *B* about $^{90}/_{1}$; *C*, *D*, *F* and *G* about $^{115}/_{1}$; *E* about $^{375}/_{1}$). (Greenland.)

fication the lateral walls are seen to be as shown in Fig. 4, *E*: pores and nodose thickenings alternate. The outer walls have fine cuticular striations. Stomata are almost equally

distributed on both surfaces of the leaf, I found them however (contrary to Wagner's statement) to be slightly in the majority on the lower surface; the absolute number per square unit proved, however, to vary somewhat, but I did not succeed in finding any fixed rule as regards this point. The stomata are on a level with the surface of the leaf.

One of the non-glandular hairs occurring on the leaf-margin and the under-side of the midrib is shown in Fig. 4, *F*; they are 2—4 celled, thick-walled and have cuticular warts on the surface. Glandular hairs with a one-celled stalk and two-celled head occur in great numbers and are equally abundant both on the upper and the lower surface of the leaf (Fig. 4, *A* and *B*). A transverse section discloses 2—3 layers of short and broad palisade-cells with rather large intercellular spaces; the spongy parenchyma consists of ovate to slightly branched cells; all the cells of the mesophyll are abundantly filled with chlorophyll-grains. Palisade tissue and spongy parenchyma are shown in surface view in Fig. 4, *C* and *D*. The mid-rib has on its under-side a thin layer of stereom.

Veronica alpina L.

Alcohol-material from Norway (Tromsö, leg. E. Warming, 21. 7. 1885; Muggrubskampen, Rörås, leg. Th. Resvoll, 29. 7. 1918) and Greenland (Nunatsuk, 11. 8. 1885; Ivigtut and Dronning Louises Ø, leg. P. Eberlin, 21. 8. 1883 and 8. 8. 1885). — Herbarium-material from Greenland, Iceland, the Færöes and Fennoscandia.

Lit.: Axell, 1869, p. 102; Lange, 1880, p. 72; 1887, p. 261; Müller, 1881, p. 270; Lindman, 1887, p. 81; Warming, 1888, pp. 31, 35, 39, 75, 87, 93 and 142; 1890, p. 204; Rosenvinge, 1892, p. 685; 1896 (II), pp. 128, 161, 168; Wagner, 1892, pp. 9 and 20; Hartz, 1894, pp. 9, 49, 50 and 57; 1895 (I), pp. 137, 170, 179, 266, 271, 288 and 304; 1895 (II), p. 335; Hartz and Kruuse, 1911, pp. 346, 359, 364, 409, 417 and 423; Jungner, 1894, p. 275; Koch, 1895, pp. 117 et seq. and

128; Norman, 1895, p. 452; Kerner, 1898, p. 350; Knuth, 1899, p. 171; Cleve, 1901, pp. 12, 16, 25, 40, 57 and 89; Eastwood, 1902, p. 292; Porsild, 1902, pp. 119, 181 and 209; 1910, p. 267; 1920, p. 140; Kruuse, 1905, p. 175; 1906, p. 248; 1911, in part IV pp. 196, 202, 229, 230, 242, 247, 255, 261, 262, besides many notes in the preceding parts; Sylvén, 1906, p. 80; Huchedé, 1907, p. 73, fig. IV, A^5, fig. VI, C^1; Schröter, 1908, pp. 221, 226, 468 and 493; Th. Resvoll, 1917, p. 208.

Nanophyllous sympodial chamæphyte with primary root which dies away early (Sylvén), and abundant development of adventitious roots from the stem-bases, this in conjunction with the fact that the older shoots gradually die away, determines the vegetative reproduction, enabling the plants to form lax, but large tufts (Kruuse, 1906, p. 248). The winter-buds either rest upon, or are slightly raised above, the surface of the ground.

The Shoot-development has been described by Th. Resvoll; it is a process of two years duration, as in the foregoing species; the first-year's part of the shoots is either erect or obliquely ascending or quite horizontal, as in Th. Resvoll's Figs. 60 and 61; most often only 1—2 cm long and bearing a few small leaves. The next year the growth of the shoot is continued in a vertical direction, while essentially larger leaves are being formed; the shoot is frequently terminated by an inflorescence; the flowers are already formed during the autumn of the first year (l. c.). Special bud-scales do not occur, the end of the axis is only protected by the uppermost pair of leaves. After the fruit has ripened, the axis dies away to slightly above the "innovation-buds"; the latter occur, however, often rather far down on the shoots, even in the axils of the very first pair of leaves, which causes the branches of the sympodia to become very short, and the stems crowded.

Of the two shoots in the axils of two opposite leaves, the one may be far more vigorously developed than the

other; this is no doubt usually the case, and then it appears to be the shoot which is turned towards the periphery of the tuft which becomes the more vigorous and floriferous. When the plant grows in damp moss, the internodes of the horizontal, first-year portions of the shoots — as mentioned by Th. Resvoll, and as I myself had an opportunity of verifying in the mountains of Norway — may become elongated, so that the shoots become almost runner-like; in this case the plant is capable of spreading considerably.

The longevity of the branches of the sympodium is greatly restricted; a growth in thickness of the axial organs, continuous for years as in *V. fruticans*, does not take place.

Adventitious Roots are developed in the second growth-period of the shoots, they arise in the neighbourhood of the nodes. The foliage-leaves are either entire or slightly serrate; I am not prepared to say whether the leaves occurring at the base of the shoots remain green throughout the winter, in the following summer they are at any rate always found in a withered condition.

The Flower. H. Müller, Lindman, E. Warming and Kerner have in the works cited above described the structure and biology of the flower, which according to these authors agree in the Alps, Scandinavia and Greenland, nor have I been able to find any differing features. "The small, dark blue flowers are at first only 2.5—3 mm in diameter, but may ultimately become 5—5.5 mm. They are protogynous-homogamous, and appear to be well-adapted to self-pollination. While the corolla is still almost tubular or funnel-shaped and consequently only slightly open, the anthers may be open and lie close to the stigma, which may be seen to be covered with pollen-grains, many of which are germinating. Afterwards the anthers are slightly removed from the stigma by the filaments bending backwards, but not so decidedly

as in *V. saxatilis*; the anthers are, indeed, not far from remaining parallel with the style, and are therefore constantly near the stigma" (Warming, 1890). Th. Resvoll records self-pollination (at Rörås, in sched.); Fig. 5, *A* and *B* show that this may easily take place; moreover, in scarcely expanded flowers I too found the anthers open and the stigma covered with pollen.

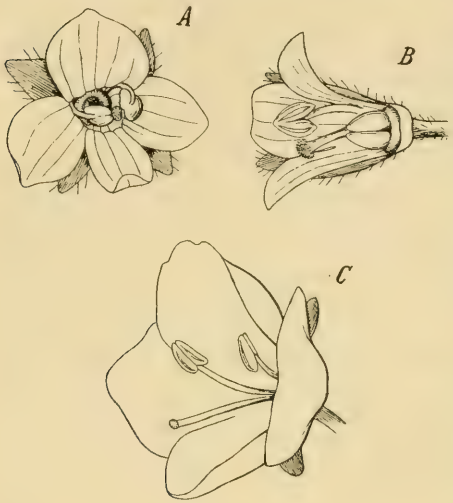

Fig. 5. *A*, and *B*, Flowers of *Veronica alpina* (Rörås, Norway, $^{29}/_{7}$). *A*, In front-view; *B*, in side-view, half of the calyx and of the corolla is removed. (About $^{5}/_{1}$). *C*, A flower of *Veronica fruticans*. (Hort. bot. Hauniens.) (About $^{4}/_{1}$.)

The ovary varies between the glabrous and finely-hairy condition.

Lindman remarks that the flowers open two at a time. They are, however, on the whole, not very conspicuous, and insect-visits are scarce.

By reason of the fact that there is no division of labour between the vegetative and purely floral shoots, the flowering period occurs late (Th. Resvoll). In Greenland *V. alpina* sets fruit abundantly, and ripens its seeds normally; the latter are scattered in autumn; wherever in Greenland *V. fruticans* and *V. alpina* occur in the same locality, the latter is always the first to flower (M. Porsild).

Geographical Distribution according to Lange: East and west coasts of Greenland, Labrador, the Rocky Mountains, western North America, Siberia, Arctic Russia,

Scandinavia to Lapland and Finmark, Iceland, Great Britain and the Alpine regions of Southern Europe. To these should be added the Færöes (Ostenfeld, 1901, p. 56). In West Greenland the northernmost limit is found on the Nugsuak-peninsula (70°42′); in East Greenland it passes over the Scoresby Sound.

Habitat. In West Greenland *V. alpina* grows in copses, on "herb-slopes", in snow-troughs (Snelejer) where the snow does not lie till very late in the summer, and on sandy flats near the shore (Warming, 1888; Rosenvinge, 1896 (II)). In East Greenland it is noted too from "herb-slopes", grassy-slopes and copses; besides, Kruuse, in the Angmagsalik district, has found it growing on the steps of steep rocks above the slopes. It is always well covered with snow during its winter-rest (cf. also Kruuse, 1905, p. 175 and Porsild, 1920, p. 140). Th. Resvoll mentions the species as a common plant of the snow-troughs in the whole of Norway; according to Norman it is also found by mountain-streams, in birch-wood glades, on inundated river-banks, on the coast and on mountain-summits. A. Cleve records: "Häufig und üppig ausgebildet in

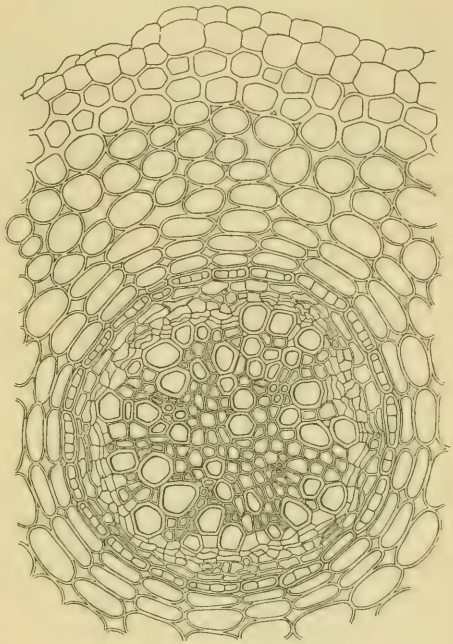

Fig. 6. *Veronica alpina.* Transverse section of an adventitious root (about $^{230}/_{1}$). (Norway.)

Sumpfwiesen, . . . Ferner häufig in der Moosmatte, dort noch mit Blüten und Knospen am $^{6}/_{9}$ und in rein vegetat. Individ. näher an dem ewigen Schnee als irgend eine andere Blütenpflanze beobachtet. Meidet dagegen entschieden trockene Heiden und Wiesen". Th. Resvoll, also, states that, in unfavourable localities, where the snow lies till late in the summer, *V. alpina* occurs as sterile specimens.

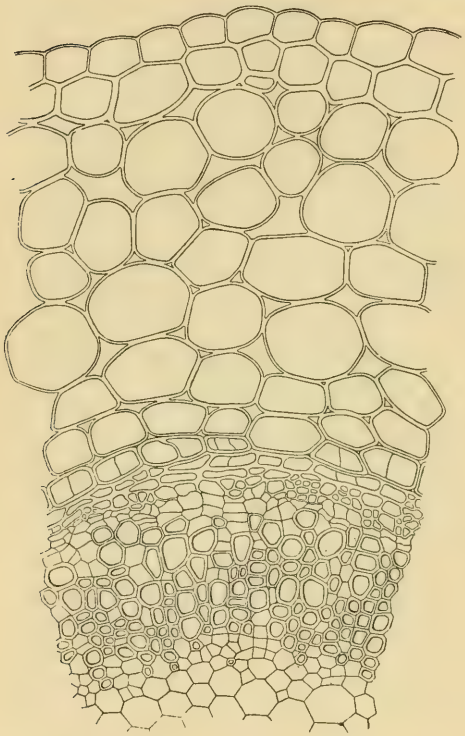

Fig. 7. *Veronica alpina.* Transverse section of a stem (about $^{230}/_{1}$). (Norway.)

In the Alps, as recorded by Schröter, the species is "einer der verbreitetsten Rasenbestandteile von der subalpinen bis zur nivalen Region (1500—3185 m in der Schweiz, 1560—2870 m in Bayern) alle Bodenarten bewohnend, indifferent gegen Düngung und Humusgehalt". Besides this, it occurs in snow-troughs (Schneethälchen).

Anatomy. The Root. The epidermis becomes cuticularised and persists a long time. The outermost layer of the cortex consists of thin-walled cells with cuticularised outer and lateral walls; the two succeeding layers within the cortex (Fig. 6), have, on the other hand, fairly thick-walled cells which unite mutually and with the exodermis

without intercellular spaces; the walls show the reaction of cellulose. During the growth in thickness of the stele, the endodermal cells are stretched tangentially, and become subdivided by 2—4 thin radial walls; the walls of the original endodermal cells show Casparian dots, but only faintly. The cortical cells contain starch; root-hairs occur in great numbers. In the xylem portion I have not found indication of annual rings (the root figured is several years old) as in the foregoing species; consequently, the roots complete their development in the course of one year. The xylem is composed of vessels and wood-fibres.

The Stem. As in *V. saxatilis* the xylem, in the first year of growth, when the shoots are but weak, frequently consists only of scattered vessels with intervening non-lignified parenchyma, and not until the second year is a continuous ring of vessels and wood-fibres formed, as shown in Fig. 7, which shows a portion of a transverse section of the basal, persistent part of the shoot. I never found more than 3 years' growth in thickness, not even in shoot-bases apparently older. The vessels are comparatively numerous, and the wood-fibres are more sparingly present and also more thin-walled than in the foregoing species. In the cells of the long-lived epidermis tannin is found; cork-formation does not take place, neither in the stem nor in the root. The cells of the cortex contain chlorophyll-grains. The young shoots are beset with glandular hairs of the same type as those on the leaf. In the upper part of the stem, which dies away after flowering, the wood-ring is of course formed entirely during one growth-period, here it is thinner than in the lower part; the cortical cells are thinner-walled and richer in chlorophyll, and the epidermis contains no tannin.

The Leaf. The epidermal cells of the upper surface have slightly, those of the lower surface more highly, un-

dulating lateral walls; they are thin and without pores (Fig 8, *D*). Stomata occur almost equally on both sides of the leaf, frequently they are slightly in the majority on the

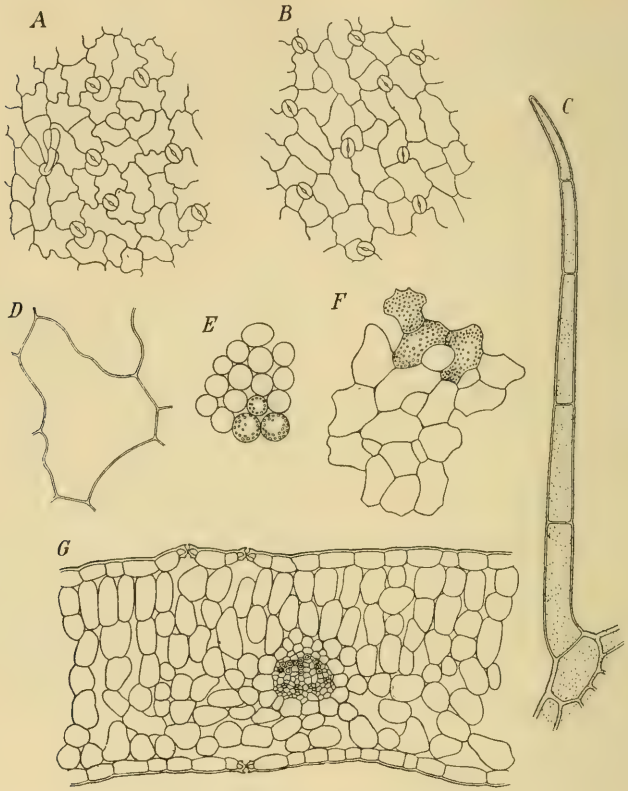

Fig. 8. *Veronica alpina.*
A, Epidermis of the lower surface of the leaf. *B*, Epidermis of the upper surface of the leaf. *C*, A non-glandular hair from the leaf-margin. *D*, An epidermal cell more highly magnified. *E* and *F*, The upper and lower layers respectively of the mesophyll, in surface view. *G*, Transverse section of the leaf (*A* and *B* about $^{90}/_{1}$; *C*, *E*, *F* and *G* about $^{115}/_{1}$; *D* about $^{375}/_{1}$). (Greenland, Dronning Louises Ø, 8. 8. 1885.)

upper surface; the stomata are on a level with the surface of the leaf. Both leaf-surfaces are furnished with glandular hairs of the usual type — a two-celled head on a one-

celled stalk; non-glandular hairs (Fig. 8, *G*) usually occur only along the leaf-margin.

The transverse section shows 2—3 layers of short and broad palisade cells with rather large intercellular spaces; the cells of the spongy parenchyma are somewhat more branched than in the foregoing species (cf. surface view, Fig. 8, *F*).

Chlorophyll-grains are abundantly present in the whole of the mesophyll; they are also found in the epidermis of the lower surface.

Veronica officinalis L.

(f. *glabrata* Fristedt).

In the collections preserved in the Botanical Museum in Copenhagen there is some material of *Veronica officinalis* collected in the Færöes, part of which belongs to the main form with hairy leaves, and part to f. *glabrata* Fristedt (Vægtgeografiska skildr. af Södra Ångermanland, Upsala, 1857). Of both forms there were individuals of normal size, as well as dwarf individuals.

The Morphology of the species has been described several times (e. g. Warming, 1884, p. 58; Brundin, 1898, p. 83), most exhaustively by the first-named author, from whose description the following is quoted: "The creeping and rooting shoots bear only foliage-leaves (evergreen); at the apex they are frequently bent slightly upwards in a curve, especially when the plant grows among moss; but gradually as the adventitious roots are developed in ascending succession, the stems are drawn down to the ground. From the basal portion of the year's shoots there proceeds shoots which resemble the parent shoot; in this species no lateral shoots are found which can be indicated as special "assimilatory shoots", which are such only, without taking at the same

time part in the vegetative propagation; from the leaf-axils which follow next, racemose inflorescences proceed. But after a short pause during the flowering period, the parent shoot continues its growth at the apex and, under favourable conditions, may also produce new lateral shoots, as also it may, it is true, continue its growth throughout the winter, as soon as the temperature has reached a certain degree of warmth. I have, however, observed several cases in which the main shoot had been biologically arrested through flowering, and had died away as far down as below the inflorescences."

Fig. 9. *Veronica officinalis* L. f. *glabrata* Fristedt. Kirkebökamp, Strömö (The Færöes). (About $^2/_1$).

A dwarf specimen of f. *glabrata* (Strömö, Kirkebökamp, leg. C. H. Ostenfeld, 8. 6. 1895) is illustrated in Fig. 9; it is drawn almost twice the natural size. The individual did not flower; the few leaves from the previous year which are still remaining, are recognizable by their being shaded. The branching is seen to be abundant — these dwarf individuals therefore often form rather dense tufts. Uppermost in the figure the last-formed leaves are seen to bend over the apex of the

shoot; the reason of this is unknown to me. Upon the oldest portion of the shoot-system which has been figured, adventitious roots are seen to be rather abundantly developed.

According to RAUNKIÆR (1907, p. 46) *Veronica officinalis* is an active chamæphyte; the species is nanophyllous, and evergreen (see above).

In "Field-notes on the Biology of some of the Flowers of the Færöes" (Botany of the Færöes. Vol. III, p. 1065) E. WARMING writes concerning *Veronica officinalis*: "The diameter of the flower is 7—8 mm. The corolla is pale-lilac with stripes of a darker colour. Homogamous. The anthers and the stigma occur at the same level, but as the stamens are spreading, insect-pollination appears to be necessary for the setting of fruit."

Geographical Distribution: Europe, Western-Asia, North-America.

According to OSTENFELD (1901, p. 57) in the Færöes *Veronica officinalis* is "Rather common in low-lying regions on hill-slopes and on rocky-ledges; also occurs at high levels and there mostly as f. *glabrata* Fristedt . . . Fl. beginning of July. Fr. August, but bears fruit sparingly; often fails altogether in the hills."

The specimen illustrated in Fig. 9 was investigated with respect to its leaf-anatomy. The epidermis of the upper surface (Fig. 10, *B*) had lateral walls, from straight to slightly undulating, and that of the lower surface (Fig. 10, *A*), rather strongly undulating lateral walls. Glandular hairs with one-celled stalk and two-celled head occurred abundantly on both leaf-surfaces. In Fig. 10, *C* some epidermal cells are shown under higher magnifying power; the two smaller and thin-walled ones have borne glandular hairs (the small

circles inside their outlines indicate the connection of the stalk of the gland with the outer wall of the cell), the lateral walls of the others are seen to be porose with nodose thickenings between the pores; in the main form I found these thickenings to be somewhat more strongly developed; they were very pronounced in individuals collected in dry habitats in Denmark. A transverse section of the leaf is shown in

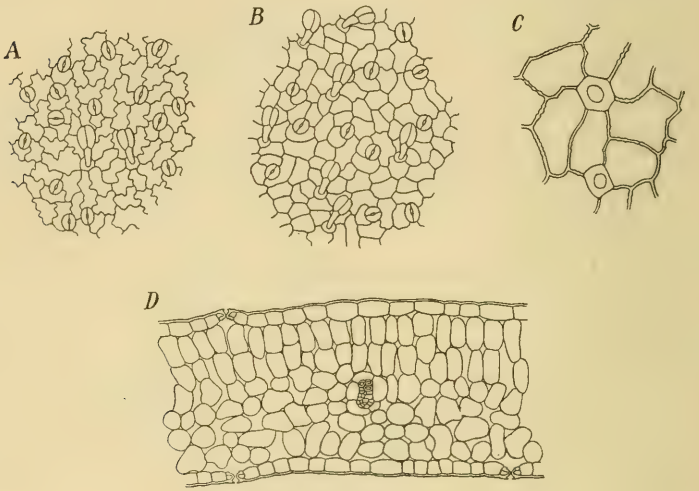

Fig. 10. *Veronica officinalis* L. f. *glabrata* Fristedt.
A, Epidermis of the lower, and *B* of the upper surface of the leaf. *C*, Epidermal cells from the upper surface of the leaf, more highly magnified. *D*, Transverse section of the leaf. (*A* and *B* about $^{90}/_{1}$; *C* about $^{225}/_{1}$; *D* about $^{115}/_{1}$). (Kirkebökamp, Strömö (The Færöes)).

Fig. 10, *D*; in the upper part of the figure there are two layers of short and broad palisade-cells; the spongy parenchyma consists of rounded or slightly branched cells. Any special difference in the structure of the mesophyll in the Færöese and the Danish plants, could hardly be demonstrated; the description given by Koch (1895, p. 134) also agrees with that given above.

Fig. 10, *A* and *B*, which are drawn from epidermis-preparations of one of the leaves with the under surface turned upward, seen uppermost in Fig. 9, show the proportion between the number of the stomata on the upper and lower surface of the leaf to be about 2 to 3; in the normally orientated leaves of the same individual, there were, however, generally about 3 times as many stomata on the lower as on the upper surface. On the whole, I always found in all the individuals of *Veronica officinalis* investigated by me, by far the greater number of stomata on the lower surface of the leaf, viz., 3 to 5 times as many as on the upper surface — this feature, as well as the absolute number of the stomata per unit of area, may however vary in the different leaves on the same individual.

The non-glandular hairs, which are found in greater or fewer numbers on the leaves and stems of the main form, are multicellular, thick-walled, and have cuticular warts.

Castilleia pallida (L.) Kunth.

Alcohol material from Kola (the Voronej River, leg. Brotherus, 2. 7. 1887) and Arctic America (King Point and Herschell Island, leg. A. H. Lindström, 1905—1906). Herbarium material from Arctic America (Port Clarence, King Point and Herschell Island (var. *unalaschkensis* Cham.), Labrador, the coast of Hudson Bay (Ranken Inlet, Churchill (var. *septentrionalis* (Lind.) Gray)), *Lapponia imandrae.*

Lit.: Lange, 1880, p. 79; E. Warming, 1890, pp. 220—223, fig. 34; Rosenvinge, 1892, p. 687; P. Knuth, 1899, p. 193; Simmons, 1913, pp. 122 and 138.

Spot-bound, nano-microphyllous, sympodial proto-hemicryptophyte with a slightly branched primary root of long duration. Only one shoot-generation reaches maturity in each growth-period. The perennial basal portions of the shoots

live for several years, and can have growth in thickness; adventitious roots are developed but sparingly. The shoots are erect and hairy especially above in the floral part; if they are capable of flowering — which ordinarily appears to be the rule — they terminate in a raceme, the subtending leaves of which are large, the lower ones similar to the foliage-leaves, but often having long lobes.

In the axils of the 4—7 radical scale-leaves (bud-scales) of the shoots "innovation-buds" occur, but of these only 1—2 are further developed; the uppermost of them appear on the whole to be the most vigorous, but none of them is a decidedly principal bud. The foliage-leaves differ greatly in shape and size in the different forms in which the plant occurs; in var. *unalaschkensis* they are large, ovate-lanceolate (50—60 mm long, as much as 17 mm broad); in var. *septentrionalis* they are smaller, linear-lanceolate 30—40 mm long, 3—4 mm broad); the principal form is intermediate. Fruits with ripe seeds occurred in my material from the localities in Labrador and Hudson Bay; the fruit ripens in July—August. The seeds are small and light with a reticulated, pitted testa; this pattern is produced by the very thin outer walls of the outermost, large-celled layer of the seed-coat, sinking down into the cavity of each cell, while to the inner and lateral walls rigidity is given by a network of anastomosing flange-like thickenings.

The structure and biology of the flower has been exhaustively described by E. Warming, (l. c.), from whom I quote the following (compare also the accompanying figure with explanation which has been taken from the paper in question): "The hairy calyx is deeply cleft into two lateral lobes, which again are cleft into a larger anterior and a smaller posterior lobe, both oblong. Here the corolla is only of about the length of the calyx, tube-shaped and two-lip-

ped. The lower lip is shorter, with three ovate obtuse lobes which are erect or slightly reflexed; at the base of each lobe the lip is inflated into a bipartite arch (*A*, *B* and *G*). The upper lip is erect, boat-shaped, and terminates in an entire apex; a little distance below the apex it is provided on

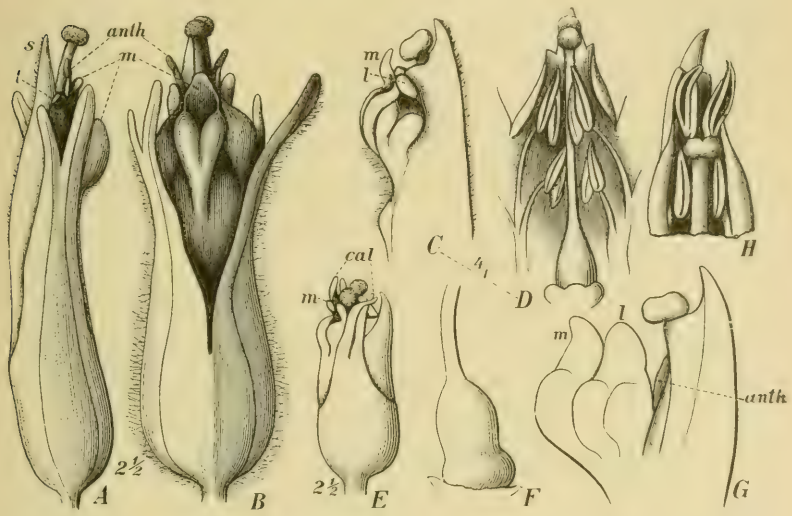

Fig. 11. *Castilleia pallida* (From Kola at the White Sea). *A* and *B*, A flower seen from the right side and from the front; the anthers (*anth.*) have grown out of the flower and are open; the stigma protrudes above them; behind it the upper lip (*s*) is seen; the middle part of the lower lip is marked *m*, one of its lateral lobes (the right one) *l*. The hairs are indicated only along the periphery. *C* and *D*, Parts of a young flower, seen from the left side and from the front, after having been artificially opened. The anthers have not dehisced; *m* is the middle lobe of the lip, *l* one of its left lateral lobes. *E*, A flower from the same inflorescence as *A*, seen from the left side, but much younger and smaller; even here the stigma is large. *F*, Ovary of *A*. *G*, Each stigma in the whole inflorescence to which this flower belongs is as much enclosed as it is here; the anthers (*anth.*) of the long stamens are open, those of the short ones are closed. *H*, The relative positions of the stamens and stigma in the lowermost flower (14 mm long) in an inflorescence; the two uppermost anthers are open and are situated just above the stigma; the next flower appears to be similar; the third one was almost a bud, but had its stigma protruding to the usual distance. (Drawn by E. Warming).

either side with a rather thin wing (*D* and *G*), which in its upper part may be erect or curved slightly inwards around the anthers and stigma, while in its lower part the edge is revolute (*G*) as in *Pedicularis*, but the revolute portion ("die Rolle") is quite smooth here. As both lips are erect and close tightly, there is, between them, a very narrow entrance to the flower, through which, on the one hand, only very small flies and other small insects can creep in, and on the other hand, only butterflies and bees with long proboscides can gain entrance into the flower. The anthers of the long stamens open before those of the short ones (*H*), and the anthers of the latter always remain enclosed, while those of the long stamens protrude more or less. Here also the style appears to vary in length; in some inflorescenses I found it protruding far, even in quite young flowers — sometimes so young that they must rather be called buds (*E*); and as the stigma here also appears to be developed early, these flowers must be called longistylous—protogynous. In other flowers I found the stigma to protrude less, but nevertheless to be higher than the anthers, while in others again the long stamens were so long that their anthers were in contact with the stigma, or even protruded above the latter (*H*)." (The author then goes on to say, that among flowers from the same inflorescence there may be some difference as regards the relative length of the style, the stamens and the corolla which apparently cannot be referred to difference in age); "in flowers such as *A*, *B* and *E* (from the same inflorescence) self-pollination will be able to take place only with difficulty, the stigma being throughout higher than the anthers and the flower standing erect, hidden behind the large bracts provided with marginal lobes. Nor will self-pollination be easy in a flower like *G*, but in flowers like

H, self-pollination will be able to take place easily, as the pollen will almost inevitably fall upon the stigma."

To the above description I can add, that in all cases, I found in fully developed flowers, with the exception only of the flowers in two inflorescences from Kola, — which happen to belong to the material upon which WARMING has based his description — the stigma projecting more or less beyond the apex of the posterior lip, usually as in Fig. 11, *A* and *B*, sometimes projecting even more, and in quite young flowers somewhat less; in several cases I verified the presence of germinating pollen upon the stigma. It has not been possible to demonstrate conditions indicative of heterostyly. It does not appear to be uncommon for the pollen, at any rate in the anthers of the two longest stamens, to germinate even before the flower has entirely expanded, i. e. while it is still hidden by the large subtending leaf, and the corolla is surrounded by the lobes of the calyx. As the stigma, even at that time, protrudes beyond the lobes of the corolla, the distance between it and the anthers will, however, in all probability be so great that self-pollination will not be able to take place; in material from Kola there was a flower, like that figured in *H*, which had germinating pollen in the anthers.

Both calyx and corolla have a dense covering of shorter and longer non-glandular and glandular hairs, similar in form to those described below under the anatomy of the leaf. According to E. WARMING (l. c.) the flowers are visited by small wasps (the genus *Pteromalus*); he found such in several flowers.

The Geographical Distribution of the plant is, according to LANGE: Labrador, Canada, the Rocky Mountains, western Arctic North America, Kamchatka, East and Arctic

Siberia, and Arctic Russia. This author records it also from Greenland, but as it has not been found since, it ought to be omitted from the flora of Greenland (Rosenvinge, M. Porsild). According to Simmons the following localities from the Arctic North American archipelago can be added: Banks Land, Baring Land, Victoria Land.

Anatomy. The Root: The epidermis dies away quickly. The primary cortex follows for a long time the growth in thickness of the stele by tangential elongation of the cells, accompanied by divisions in these by radial walls. During the secondary growth the cambium forms outwards a large amount of parenchyma, arranged in very regularly radiating rows, while the formation of sieve-tissue is extremely sparing. The cells of the parenchyma are entirely filled with starch. In the woody parts the single growth-zones are easy to distinguish, in an inner narrow portion of the annual ring the vessels being surrounded by thin-walled cells, while in the outer larger part the vessels are accompanied by wood-fibres. Also in the thin-walled cells in question starch occurs. Parenchyma-rays are absent.

The Stem: As shown in Fig. 12, *A* and *B* the ring of wood in the lower, persistent part of the year's shoots is considerably thicker than in the upper, perishable part. In that part of the stem, from which the section shown in Fig. 12 *A* is taken, the epidermis, together with the outermost thick-walled cortical layer connected with it without intercellular spaces, has partly separated from the rest of the cortex; this happens especially at the nodes, thus a leaf occurred on the axis just above the plane of the section on the side turned upwards in the figure. At the base of the shoots slits are formed at some depth in the cortex (Fig. 12, *B* and *C*); this explains the fact that the cortex can so easily be rubbed off in flakes. The persistent basal portions of the

shoots have growth in thickness, but probably only to a very limited degree. In Fig. 12 *C* two annual-rings are seen, the last-formed is very excentric, the fact often being that the most vigorous growth in thickness takes place on that side of the stem which is opposite to a developing bud.

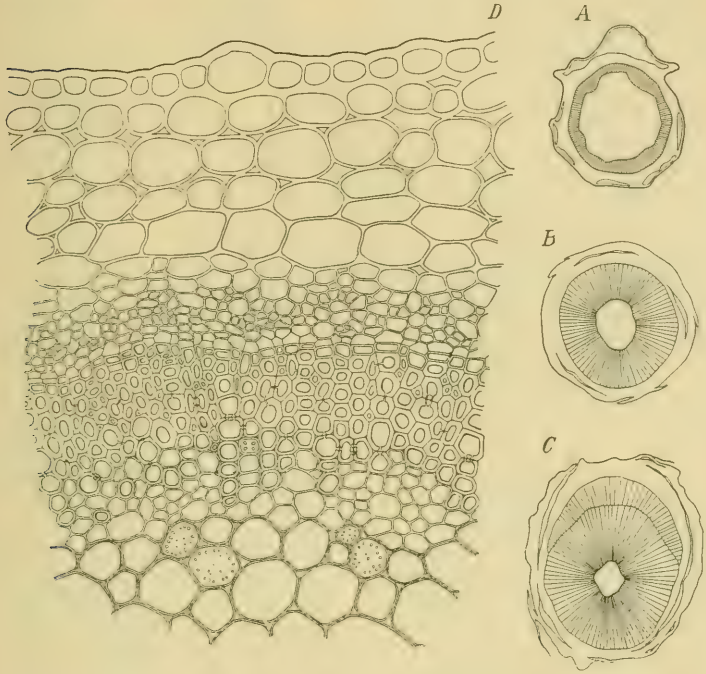

Fig. 12. *Castilleia pallida.*
A and *B*, Transverse sections of the stem of the year's shoot; *A* is taken from half-way up the stem, *B* from near the base. *C*, Transverse section of a 2-year-old, persistent stem-base. *D*, A portion of *A*, more highly magnified. (King Point.) (*A*, *B* and *C* about $^{10}/_{1}$; *D* about $^{230}/_{1}$.)

Fig. 12 *D* represents a part of *A* more highly magnified, the epidermis and the outermost layer of the cortex is thick-walled; the cortex is few-layered, its cells contain chlorophyll-grains; stomata occur in the epidermis. The endodermis is only demonstrable by faint Casparian dots.

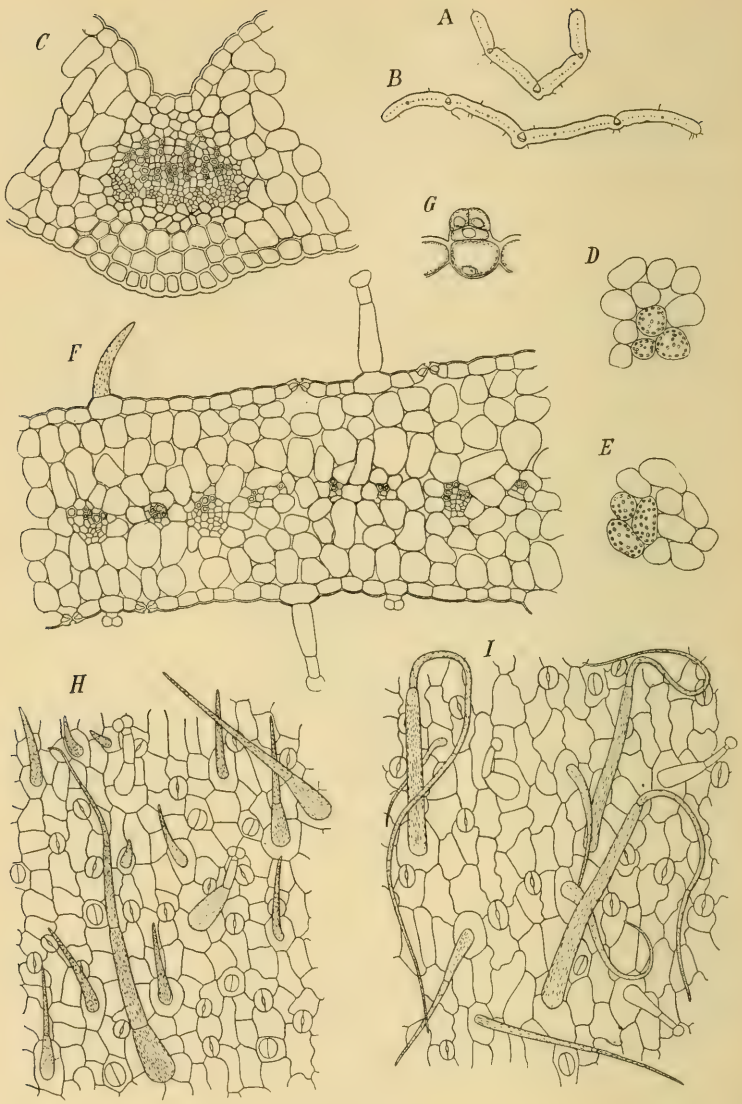

Fig. 13. *Castilleia pallida.*

A and *B*, Transverse section of leaves ($^5/_1$). *A*, var. *septentrionale* (Churchill); *B*, the principal form (Kola). *C*, Transverse section of the midrib of the leaf (Kola). *D* and *E*, The uppermost and lowermost layers of the mesophyll, seen in surface view. *F*, Transverse section of leaf. *G*, A glandular hair, more highly magnified. *H* and *I*, Epidermis from the upper and lower surface of the leaf respectively. (*D*, *E*, *F*, *H* and *I* King Point; *G* Kola.) (*C*, *D*, *E*, *F*, *H* and *I* about $^{90}/_1$; *G* about $^{220}/_1$.)

In the wood, medullary rays are entirely wanting (the radiating lines in Fig. 12, *A*, *B* and *C* indicate only the radial arrangement of the elements); exteriorly, the ring of wood consists chiefly of wood-fibres; interiorly, vessels become more frequent, and are accompanied by partly lignified parenchyma. In the basal portion of the stem the vessels are relatively more numerous than shown in Fig. 12, *D*, and the cells of the stereom are thinner-walled. The pith consists exteriorly of lignified, rather thick-walled, distinctly porose, axially elongated parenchymatous cells, towards the centre the cells of the pith are thinner-walled, non-lignified and die away, so that the stem becomes hollow.

The Leaf: Any difference as regards anatomy could scarcely be demonstrated in the leaf-types of the different forms. Transverse sections, slightly magnified, of the leaf of var. *septentrionale* and of the principal form are shown in Fig. 13, *A* and *B*, the three main veins and the numerous fine anastomoses are seen.

The vascular bundle of the main veins has on its under side a covering of somewhat collenchymatously thickened elements; on the upper side the surface of the lamina dips down towards the vascular bundle. The structure of the mesophyll is fairly homogeneous, thus in Fig. 13, *F* it is hardly possible to demonstrate a palisade-layer; in specimens from Kola the uppermost layer of the mesophyll was however elongated in a somewhat palisade-like manner. Chlorophyll-grains occurred abundantly in the entire mesophyll, and besides this they were found in the epidermal cells of both surfaces.

The epidermal cells of the upper surface have from straight to slightly undulating lateral walls, those of the lower surface can be more strongly undulating. Both the outer and lateral walls of the epidermal cells are thin; the cuticle

of the outer walls is but slightly developed. Stomata occur in almost equal number on both sides of the leaf; the guard-cells are surrounded by 4—5 cells, and are on a level with, or slightly raised above, the surface of the lamina — on the large subtending leaves of the flowers I found them sometimes raised high above the surface.

The leaves are densely covered with hairs; the following types of hair occur: (1) Non-glandular, thin-walled, pointed and with fine cuticular striations; they may either be short (1—2 celled) or long (multicellular) and even elongated like a whip, the last-mentioned are numerous especially in var. *unalaschkensis*, and particularly in the top of the shoots. (2) Glandular hairs with multicellular stalk, and with 1—2 celled head; the basal cell has sometimes cuticular striations. (3) Glandular hairs with unicellular, quite short stalk and 2-celled head (in Fig. 13, *G* such a hair is seen in lateral view, highly magnified; in *H* and *I* they are seen from above), in the cells of the head and the stalk comparatively large nuclei occur, and a highly granular protoplasm. These various forms of hair occur intermixed (cf. Fig. 13, *F*, *H* and *I*); they are also found on the surface of the stem and, as already mentioned, in the floral region.

Euphrasia arctica Lange.

(*Euphrasia latifolia* (Pursh) Wettst.)

Alcohol material from West and East Greenland (Fredrikshaab, leg. Rosenvinge, 15. 8. 1886; Sydpröven; Hekla Havn, leg. N. Hartz, 13. 8; Unartok and Tasiusak).

Herbarium material from West and East Greenland, the shore of Hudson Bay, Northern Norway, *Lapponia murman.*

Lit.: Lange, 1880, p. 79; 1887, p. 264; Warming, 1886, pp. VII and 43; 1888, pp. 34 and 59; 1890, p. 226; Rosenvinge, 1892, p. 687; 1895 (I), p. 68; 1895 (II), pp. 162, 168, 219 and 245; Hartz, 1894,

pp. 9, 15, 20, 46 and 57; 1895 (I), pp. 146, 170, 179 and 289; 1895 (II), pp. 335, 359, 372 and 377; Hartz and Kruuse, 1911, pp. 359, 364, 409, 416, 423 and 428; Wettstein, 1896, p. 136; Abromeit, 1899, p. 46; Dusén, 1901, p. 40; Porsild, 1902, p. 197; 1912, pp. 382 and 387; 1920, p. 141; Kruuse, 1905, p. 176; 1906, p. 250; 1911: in part IV, pp. 196, 229, 242, 247 and 261, and besides these many notes in the preceding parts; Jørgensen, 1919, p. 99.

As regards the Morphology, Biology and Anatomy of the *Euphrasia* spp. see: Müller, 1881, p. 279; Hovelacque, 1888, pp. 400, 454 and 477; Lindman, 1887, p. 81; Koch, 1895, pp. 140—144; Wettstein, 1896; Heinricher, 1898 and 1902; Knuth, 1899, pp. 202—206; and Kerner, 1900.

Nanophyllous therophyte; the seed germinates during early summer.

The main root is rather scantily branched; above the cotyledons there are 1—3 pairs of leaves separated by rather long internodes; "the first flowers generally occur in the axils of the 3rd or 4th pair of leaves, frequently in that of the 2nd pair, more rarely not until in that of the 5th, and as an exception, even in that of the 1st pair" (Jörgensen). Towards the apex of the stem, the distance between the leaf-pairs becomes very short; the leaves become broader, and their teeth longer and more pointed than are those on the lower leaves of the stem; they all subtend flowers. The branching is, as a rule, scanty; sometimes a few weakly-developed branches are seen to proceed from the uppermost pair of leaves below the inflorescence; occasionally, however, branches, almost as vigorous as the main axis, may be developed from the axils of the two lowermost pairs of leaves — in this case it is evidently a matter of rather late-flowering individuals (August—September). Stem, leaves and calices are more or less densely covered with hairs.

"Die Pflanze variiert sehr viel, von sehr klein und einfach, mit wenigen Blüthen — so häufig an der Witterung

ausgesetzten alpinen Standorten — bis sehr gross, grob und verästelt mit sehr grossen und breiten, grobgezähnten Blättern, die bis über 2 cm lang und ebenso breit werden" (Jörgensen). Similar variations were found in the Greenland material. From the above-said it follows that the individuals generally agree in habit with the growth-type indicated by Wettstein as "frühblütige Form" (l. c. Fig. 1, p. 44); the comparatively short period of vegetation with which the individual may be compelled to be satisfied, in consequence of the geographical distribution of the species, makes, as Jörgensen (l. c. p. 104) remarks, this growth-type necessary in Arctic regions.

The flower-morphology and -biology of the *Euphrasia* spp. have been described so often that I can here confine myself to the following remarks: *E. arctica* belongs decidedly to the small-flowered forms; in no case did I find the corolla to be more than 7 mm in length, more frequently it was shorter. The flowers are protogynous, and in the recently expanded flower, the stigma generally stands somewhat in front of the anthers, afterwards the style curves downwards and backwards, so that the stigma is brought into close contact with the anthers which are now quite open (Warming, 1890). Sometimes, however, the stigma, even at the time when the flower is expanding, is so near to the anthers, that self-pollination must be able to take place easily; I even found pollen on the stigma of a not yet expanded flower.

Warming (1890, p. 227) mentions that a length-increment of the corolla-tube can take place — as in larger-flowered species —, by which the anthers are carried forward and approach the stigma; in some few of the flowers I did find the stigma protruding so far that a movement of this kind may very probably be of importance.

Geographical Distribution according to Jörgensen:

Greenland, Cumberland, Labrador, Iceland, the Færöes, Scotland, Sweden southwards to Herjedalen and Jämtland, Norway (common towards the north, rare south of the Trondhjem Fjord), Northern Finland and Russia, in Siberia at least as far towards the east as Jenisei. Porsild (1912, p. 382) records the northern limit of the species in West Greenland to be Tartusaq (71°25′ N. lat.). In East Greenland *E. arctica* extends almost to 74° N. lat. (Lille-Pendulum Island: Dusén); from the district of Angmagsalik northwards it occurs most frequently, and grows more luxuriantly at the head of the fjords, whilst it is rarer and stunted in growth along the coast outside the fjords and on the islands off that coast.

The Habitat is given by the various authors in unison as being willow copses, heaths, grassy slopes and "herb-slopes"; Rosenvinge (1896 (II), pp. 219 and 245) also found the species growing on gravelly flats (Igaliko) and on knolls in mossy bogs; Hartz found it in the district of Scoresby Sound flowering as late as the middle of September. The fruit-setting appeared everywhere to be abundant and good.

The Anatomy of the root and the stem has been very exhaustively described by Hovelacque as regards "*E. officinalis*"; in *E. arctica* I found nothing which differed from his description.

The Root has only a few root-hairs; the cortex is thin and few-layered (3—4 cell-layers in thickness), its elements are greatly elongated in a tangential direction; in the endodermis the Casparian dots are distinct; in proportion to its diameter, the xylem part in the full-grown root forms a very thick bundle, composed of rather thin-walled vessels and wood-fibres.

The Stem has a rather thick-walled epidermis, upon which occur 2—3 celled, non-glandular hairs with fine cuti-

cular striations, and small glandular hairs with one-celled stalk and two-celled head. The cortex is few-layered (3—4 cell-layers in thickness) as in the root; in the endodermis the Casparian dots are faint, but nevertheless demonstrable

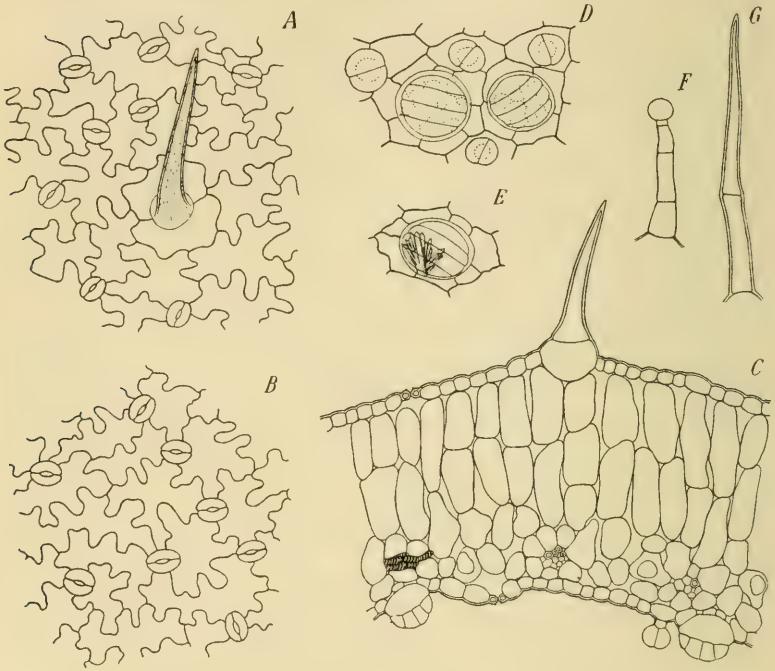

Fig. 14. *Euphrasia arctica.*
A, Epidermis of the upper, and *B* of the lower surface of the leaf. *C*, Transverse section of the leaf. *D* and *E*, Glandular hairs from the lower surface of the leaf. *F*, A glandular hair from the margin of the leaf. *G*, A 2-celled, non-glandular hair. (*A*, *B*, *C*, *D*, *E*, *F* and *G* about $^{110}/_{1}$). (Greenland.)

with Sudan III. The pericycle is 1—2 layered. The outer part of the rather broad ring of xylem is composed exclusively of wood-fibres. The peripheral cells of the pith have somewhat thickened walls. Medullary rays are absent.

The Leaf. A transverse section of one of the lower foliage-leaves is shown in Fig. 14, *C*; there occur 1—2 layers

of short palisade-cells, with rather large intercellular spaces; the spongy parenchyma consists of only slightly branched cells. The mesophyll of the upper leaves of the stem (i. e. the leaves subtending the flowers) appears, on the whole, to be more lacunose in structure than that illustrated in Fig. 14, *C*.

The margins of the teeth of the leaves are somewhat bent over, whereby a concavity is produced on their under side. In this concavity the leaf-surface is densely covered with glandular hairs, and the cells of the epidermis differ in character from the other epidermal cells of the leaf. For whilst these, both on the upper and lower surface — and especially on the upper side of the teeth of the leaves — have strongly undulating lateral walls (Fig. 14, *A* and *B*), which only here and there show a small flanged thickening, the epidermal cells in the concavities, and especially those which bear the glandular hairs, have straight or only slightly wavy lateral walls (Fig. 14, *D* and *E*), which are often (not, however, in the places illustrated in Fig. 14, *D*) furnished with flanged thickenings, the one by the side of the other. Stomata are almost equally abundant on both leaf-surfaces, in the concavities of the lower side of the teeth, however, they are less frequent; the guard-cells are on a level with the surface. In the teeth the veins break up into a fine network of tracheids.

The glandular hairs which occur on the lower side of the teeth are of two types: (1) a smaller one with one-celled stalk and two-celled, globular head, and (2) a larger one with two or more frequently four-celled cupola-shaped head, seated upon a short and broad stalk-cell which partly sinks below the leaf surface, the inner-wall of the stalk-cell, during the development of the hair, becoming rounded inwards, thus pressing the layer of epidermal cells, situated under the stalk-

cell, in the same direction (Fig. 14, *C*). The stalk-cell of the latter type of hair rests upon the connecting parts of 4—8 epidermal cells, which are produced by the division of a single cell, viz., the epidermal cell which has been the mother-cell of the glandular hair. Below the stalk-cell small, circular intercellular-spaces are formed between the lateral walls of the cells of the epidermal layer (cf. Fig. 14, *C* and *D*; in *D* that part of the lateral walls of the epidermal cells which lie under the stalk-cells, is indicated by dotted lines — the dotted circle inside the head of the small glandular hairs indicates the outline of the stalk-cell).

These large, peltate glands appear, therefore, to belong to the same type as the "Schilddrüsen" of *Lathraea* (and *Bartschia*), the development of which has been so thoroughly described by Scherffel; the intercellular spaces in the layer under the stalk-cell have not been perceived by Hovelacque or Wettstein.

The small glandular hairs belonging to type 1 are also found in other places on the leaf, but nowhere in such abundance, as in the concavities on the under surface of the teeth.

Glandular hairs with 1—2 celled head and multicellular stalk (Fig. 14, *F*), such as those required for the diagnosis of species, are found both along the margin of the leaf and also — but scantily — upon the lower surface.

Non-glandular hairs occur upon both leaf-surfaces, and are especially numerous towards the margin and on the veins; they are most frequently one-celled, but can also be 2—3 celled, pointed, and have fine cuticular striations (Fig. 14, *A*, *C* and *G*; *C* and *G* are seen in optical section; the thickness of the walls is evident from the figures). The epidermal cell or cells (2—4) which bear them are distinguished from the surrounding cells by having less strongly undulating lateral walls, and outer-walls which are more or less strongly arched outwards.

In the concavities on the under surface of the teeth I found the epidermis covered with crystal aggregates, which proved to consist of calcium-carbonate. — The same observation has been made by Wettstein (l. c. p. 19). I have sometimes also found crystals of the said substance in the cells of the large glandular hairs, as shown in Fig. 14, *E*.

The palisade-tissue and spongy parenchyma were rich in chlorophyll-grains; and such were also found in the epidermis of the lower surface.

Bartschia alpina L.

Alcohol material from Norway (Aursundsöen, leg. Th. Resvoll, 31. 8. 1918; Bosekop, Kaafjord, Alten, leg. E. Warming, 11, 17. 8. 1885), Greenland (Sukkertoppen, 5. 7. 1884; Lyngmarken, leg. L. K. Rosenvinge, 25. 7. 1886; Kangerdluarsuk, 5. 8. 1884 and 30. 7. 1885; Holsteinsborg, 15. 7. 1884; Sarfanguak, 15. 7), and Iceland (Gullfos and Tungafos, leg. A. Feddersen, 25. 6. and 30. 6. 1886).

Herbarium material from Fennoscandia, Island of Kolgujew, the Færöes, Iceland, Greenland, the coast of Hudson Bay.

Lit.: Axell, 1869, p. 102; Lange, 1880, p. 78; 1887, p. 263; Müller, 1881, p. 283; Warming, 1886, pp. II, VI, 7 and 43; 1888, pp. 34, 39, 67, 75, 93 and 188; 1890, p. 226; Lindman, 1887, p. 82; Hovelacque, 1888, pp. 403, 451 and 478; Rosenvinge, 1892, p. 687; 1896 (II), pp. 128, 144, 161, 165 and 168; Hartz, 1894, pp. 9, 15, 27, 43, 57; 1895 (I), p. 302; 1895 (II), pp. 359, 372 and 392; Jungner, 1895, pp. 224 and 238; Norman, 1895, p. 455; Abromeit, 1899, p. 45; Knuth, 1899, p. 197; Kerner, 1900, Bd. I, pp. 107, 129, 131 and 32, 173 and 606; Bd. II, pp. 116, 156, 251 and 301; Cleve, 1901, pp. 8, 9, 23, 40, 57, 71, 76 and 89; Heinricher, III, 1901; Porsild, 1902, pp. 181 and 194; 1912, p. 382, 387; 1920, p. 141; Kruuse, 1905, p. 177; 1906, p. 249; 1911: in part IV, pp. 202, 229, 242, 244 and 254, and besides these numerous places in the preceding sections; Sylvén, 1906, p. 86; Hollstein, 1907, p. 126; Schröter, 1908, pp. 465—68 and 772.

A nanophyllous to microphyllous proto-hemicryptophyte with subterranean runners; the shoot-development usually extends over 2 years.

According to Heinricher and Sylvén the seed germinates in early summer. The first-named author, who has studied *Bartschia* very thoroughly, has pointed out that it belongs to the comparatively few plants which produce buds in the axils of the cotyledons. Whilst the uppermost part of the primary shoot dies away, the following year one of these buds develops into a foliage-leaf-bearing shoot, in the basal portion of which, small innovation-shoots arise, which, like their parent-shoot, will continue their growth in their second year, and become foliage-leaf-bearing shoots. As was the case with the primary shoot, the uppermost part of the axes of the succeeding shoot-generations dies down to above the innovation-shoots. Even after the 4th vegetative period, Heinricher's cultures did not yet bear flowers; the young plants had formed small sympodial, subterranean rhizomes, composed of the persistent, basal portions of the innovation-shoots.

Heinricher is of opinion that, in Nature, the first vegetative-stage is of 4—5 years duration.

With regard to the morphology of the full-grown plant, in the following description the statements given in the cited work of Heinricher will be found verified; for criticism of preceding investigations (Hovelacque, Kerner), reference may be made to the same author.

Fig. 15, *A* and *D* show the structure of the shoot, and the mode of branching. In Fig. 15, *A*, each of the two shoots, II^1 and II^2, had terminated in an inflorescence. The shoots are in their 2nd year of development; during the first year each of them had developed a subterranean portion, bearing decussated scale-leaves which have now withered; the uppermost pairs of these scale-leaves has served as bud-scales for the winter-buds. The first year's growth-increment especially of II^1 is seen to have the character of a runner, the growth-

direction has been horizontal, and the distance between the nodes is comparatively considerable. The apex of such a runner is shown in Fig. 15, *C*. In Fig. 15, *D*, *III*^{2} has not borne flowers; the sister-shoot *III*^{1} has been arrested in its

Fig. 15. *Bartschia alpina.*
A, The lower portion of a flowering plant; both *II*^{1} and *II*^{2} have borne inflorescences (Holsteinsborg, 5. 7. 1884). *B*, A foliage-leaf. *C*, The apex of a runner. *D*, Portion of a sympodium in which the runner-like portion of shoot *II* is particularly long; *r* is an adventitious root. (*C* and *D*, Aursundsöen, 31. 8. 1918.) (About $^4/_3$.)

development, the two small basal pairs of leaves are from the previous year, and withered, but the bud is in a fresh condition; like shoot *II* shoot *I* has had a long runner-like portion. The innovation-shoots are always developed from the portion of the shoot of the first year; in case the latter

shoot is elongated in a runner-like manner, the new shoots generally appear near the spot where it begins to bend upwards, but if it is short and vertical, the new shoots most frequently appear at the base — sometimes, however, also higher up; as an exception, shoots ("enriching-shoots") may appear in the axils of the lowermost foliage-leaves: such shoots, however, will probably be always purely vegetative and terminate their development in the same year as the parent-shoot. After flowering and fruit-setting, the latter shoot dies down to immediately above the innovation-shoots.

Innovation-shoots are generally developed to the number of two on the parent-shoots; II^1 and II^2 in *A* and III^1 and III^2 in *D* are seen to have arisen in the axils of two opposite scale-leaves; this is most frequently the case, and explains the fact why two flower-bearing axes are frequently found to stand together. In Fig. 15, *D* a non-expanded bud is seen in the axil of the first scale-leaf to the right of the subtending leaves of the innovation-shoots.

The innovation-shoots are developed rather late in the Arctic summer; in the abundant herbarium-material from Greenland which I have at my disposal I never found the young shoots to be visible in individuals collected in June—July, whereas in those collected in August they were about one centimetre long.

This does not quite agree with the statement of Heinricher, according to which they already expand simultaneously with the foliage-leaves of the mother-shoot. The difference may perhaps be explained by the more unfavourable conditions of growth, presented by the Arctic summer, in which the building-up of new organs can be compelled to extend over a longer space of time.

The same author states, that small buds for the innovation-shoots are already to be found the year previous to

that, in which they expand; the same is the case with the buds for the flowers.

As already mentioned, the portion of the shoot developed during the first year of growth, may either have elongated internodes and be runner-like, or — as e. g. figured by KERNER on p. 129 (l. c.) — it may have quite short internodes with close-set scale-leaves; the first 2—3 internodes of the stem are, however, generally somewhat longer than those following; and here the scale-leaves are smaller. If by means of the latter form of shoots the ramification should be continued through several shoot-generations, the individual becomes gradually cæspitose in habit. A tuft of this kind collected by M. PORSILD in West Greenland ("heathy slopes") had about 50 older and withered shoots, and some 20 fresh ones — both vegetative and flowering. The individual had sometimes formed quite short runners, adventitious roots were scantily developed, and the entire system was borne by a single root (whether main root or adventitious root was not clear) about 5 mm thick.

The adventitious roots spring — often abundantly — from the nodes.

The rhizome, probably as a rule, dies away rather quickly from behind; however, in a specimen from East Greenland with cæspitose habit, a part of it had attained a thickness of fully 5 mm, and the whole system was evidently old.

The plants are densely covered with hairs especially at the top; hairs (non-glandular) also occur on the subterranean portions of the shoots, KERNER ascribes importance to these hairs as organs of absorption; according to HEINRICHER, however, there is no reason to assume that they have such a function.

The Flower-biology has been dealt with by H. MÜLLER, E. WARMING, LINDMAN, KERNER and others. The accompa-

nying figures are borrowed from Warming, 1886, and the following is cited from his description: "The Scandinavian and Greenland individuals of this species appear to me to be exactly alike in every way, but differ from those of the Alps in at least one respect, that is, provided that H. Müller has informed us of all the forms occurring there. Fig. 16 shows

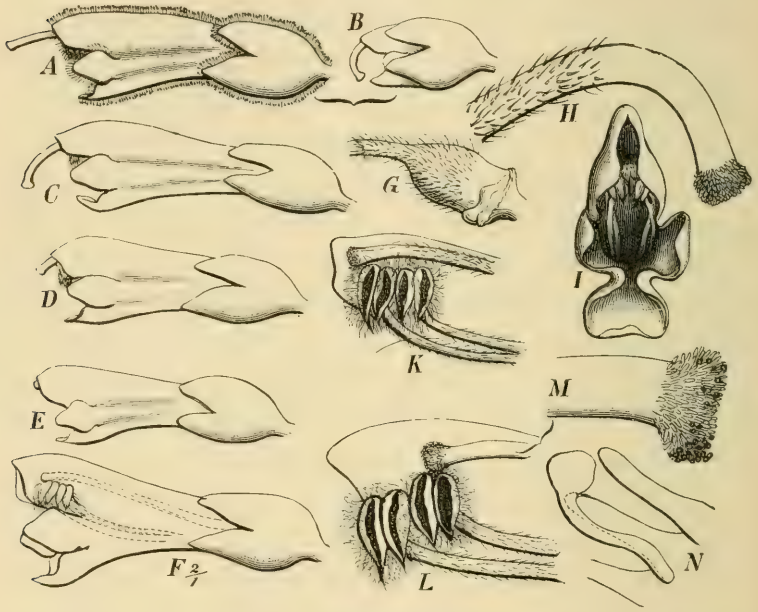

Fig. 16. *Bartschia alpina.*
A and *B* from East Greenland (Eberlin, 30. 7. 1885); *C* from Kaafjord near Alten in West Finmark; *D* from Godthaab in West Greenland (28. 6. 1884); all the anthers were open, and pollen had already germinated upon the stigma. *E* and *F* are from Holsteinsborg in West Greenland (15. 7. 1884). *A*—*F* are twice the natural size; the others, which are all drawn from Greenland material, are in various magnifications. For further particulars see text (Warming, 1886).

the structure of this flower, partly from Norwegian and partly from Greenland material (in the majority of cases the hair-covering has been omitted or only indicated along the outlines of the figures). The conspicuousness of the dull purple-violet

corolla, which like the calyx, is densely covered with glandular hairs, is increased by the fact that the subtending bracts are also of a dull violet. I have not noticed any scent, but honey is secreted by the greenish nectary on the front of the ovary (Fig. 16, *G*). Müller has described how humble-bees and other insects, by thrusting their proboscis and also their heads into the flower (see Fig. *I*, the corolla seen from the front) strike against the pointed lower ends of the anthers (Fig. 16, *K* and *L*), whereby the anthers which adhere by their hairs, are violently torn from one another, by which means the dry and light pollen-grains are scattered and fall upon the insect, which then easily conveys them to another flower and deposits them upon the stigma (Fig. 16, *A*—*E*, *M*) which protrudes even in the bud (Fig. 16, *B*). Specimens with flowers, the structure of which is exactly like that of the flowers of the Alps, have also been found to occur both in Norway and in Greenland[1], these specimens have evidently marked insect-visited flowers which either cannot pollinate themselves, or can only do so with great difficulty. My figures (which have all been drawn from full-grown flowers) show that both the length of the style and the size of the whole flower vary considerably, apart from the difference of age. Thus specimens are found which have so short a style throughout their whole life, that the stigma does not become visible outside the corolla; in some, however, the stigma is situated immediately inside the throat of the flower (Fig. 16, *F*, *K*), but in others it lies even as far inside as above the hindmost anthers (Fig. 16, *L*). In these cases the stigma lies against the anthers, and self-pollination, as far as I can see, is inevitable; and in such flowers I have also distinctly seen

[1] Müller does not mention that the style is beset with stiff hairs directed forwards, except at its uppermost end (Fig. 16, *H*); but it is probable that it has this feature also in the Alps.

pollen-grains deposited especially upon the lower part of the stigma — the part which is in contact with the anthers (Fig. 16, *M*). For the rest, the pollen-grains fall out very easily, and it is very common for masses of pollen-grains to be found scattered everywhere in the flower: on the corolla, the filaments, the style, etc. Even if the stigma ripens shortly before the anthers — which I found to be the case in the district of Holsteinsborg — the two organs nevertheless very soon become simultaneously functional and this throughout the greater part of the life of the plant, so that self-pollination is possible. That *Bartschia*, in many places in Greenland, produces ripe fruit, I saw in 1884, from the fragments of such fruit which had remained over from the preceding year."

According to Kerner (II, p. 301) wind-pollination takes place regularly in *Bartschia*, in a similar manner as for instance in *Lathræa*, at the end of the flowering period: the style in the older flower withers, the filaments are elongated and carry the anthers outwards, the latter separate and pollen, which may have been left in the anthers is scattered by the agency of the wind, and may pollinate the younger (upper) flowers of the inflorescence. This probably explains the fact mentioned by Lindman that the anthers may project beyond the edge of the corolla. This author also mentions the same variations in the length of the style as those of which Warming speaks.

Also in the material at my disposal there were flowers in which the anthers protruded, and it was generally the lowermost (oldest) flowers of the inflorescence in which this was the case.

Aug. Schulz differs from Warming in finding that in the Riesengebirge (Bibl. bot. No. 10, 1888, p. 74 — here cited from Knuth) the length of the style, in relation to the corolla,

differs in older and younger flowers, so that the style of the younger flower protrudes farther than that of the older, the corolla-tube of the latter having increased in length. The elongation may be as much as 5 mm and bring the anthers — the filaments follow the corolla in growth — into contact with the stigma, so that self-pollination takes place. Warming (1890, p. 226) admits that such a growth can take place, and disturb the relations of the organs in question, but maintains that individual differences also occur in the relative length of the style and the corolla. I found the same forms that have been illustrated by Warming (1886) in his Fig. 3, *A—F*, *K* and *L* (reproduced in this paper as Fig. 16), and even if there might possibly occur some difference in the length of the corolla of older and of younger flowers of the same inflorescence, yet I never found the style protruded far in the young flowers and enclosed in the older ones; that, at any rate under more northerly latitudes, it is really a matter of individual differences, is supported by a statement of Mr. Nyhuus of Tromsö, who in a letter to E. Warming in 1885 writes: "On Aug. 24th I found *Bartsia* there (i. e. Dalfjæld in Marknæsdalen) in abundance (towards the south) from a height of 2500 feet and down over the whole mountain; but from about 2500 to 1500 feet I did not find a single flower with protruding style although I can truthfully say that I examined several hundred plants. On the other hand, lower than that, long-styled flowers became constantly more frequent" (E. Warming, 1886, p. 10).

I found the fruit-setting to be good and abundant everywhere. "Die geflügelten Samen werden durch den Wind verbreitet." (Schröter).

Geographical distribution in the Arctics according to Lange and Porsild: Labrador, Arctic Russia and Siberia, (according to F. R. Kjellman's lists of the flora, in Siberia

it does not seem, however, to occur at or near the coast), Scandinavia, Iceland, the Færöes and Great Britain, in addition, the species extends over "ein mittel-europäisches Gebirgsareal von den Pyrenäen bis zum Balkan mit Vorstössen zu den deutschen Mittelgebirgen und zahlreichen Standorten im Vorland" (Schröter). In West Greenland its northern limit is the Ignerit Fjord (Umanak), in East Greenland it does not reach so far as to the region of Scoresby Sound. Kruuse (1905, p. 177) states that the northern limit there is at 68° 8′ N. lat.

Habitat. According to Warming in West Greenland it grows in willow-copses and on "herb-flats"; in the most southerly West Greenland Rosenvinge found it in willow and birch copses, on "herb-slopes" and grassy slopes.

As regards the conditions pertaining to the growth of *Bartschia* in East Greenland Kruuse (1905, p. 177) writes: "it is very rare north of 66° 20′ and only 10 cm. high, but yet it sets flower everywhere and as far as can be judged from the collected material also fruit. It shuns here the coast, and all finding places are well sheltered, exposed to the south and have the character of herby slopes, while the species more to the south prefers heath", and in the Angmagsalik district it is (1906, p. 249) "commonly distributed on herby slopes and in fertile heath".

Norman records it from Northern Norway as growing "in bogs, on damp cliffs, in birch-woods, on flats at the river-banks and on the beach, as an exception below the uppermost belt of sea-weeds; it occurs chiefly on the sunny sides, somewhat more seldom on the indifferent (eastern and western) sides and as an exception on the shady sides". A. Cleve records that on the mountains in the north of Sweden it is "Ein sparsamer, exclusiver Bewohner der trockenen Blütenwiese mit vollen S-Exposition . . . Ein typischer hydrophyt

der Weiden- und Waldregionen Lapplands, kann aber diese Art im Hochgebirge sich nur an den viel Wärme darbietenden Stellen behaupten, mögen letztere auch viel trockenen sein, als es gewöhnlich in dem Tieflande der Fall ist."

In the Alps it grows on "alle Formen alp. Wiesen und den Quellfluren von den Vorbergen bis gegen die Nivalregion (Schröter)".

In the Arctics *Bartschia* belongs to the group of plants of later summer, which is easily understood when one considers the considerable vegetative work the shoots must carry out, before flowering can take place.

Anatomy. The Root. An adventitious root, about 1 mm thick, showed the following structure: The epidermis had died away, only here and there a few of its cells remained in a collapsed condition. The outermost layer of the primary cortex had cuticularized cell-walls; in many of its cells a division had taken place during growth, and in these cells one very thin, non-cuticularised radial wall was found. The cells in the inner layers of the cortex were distinctly tangentially elongated and were likewise divided secondarily by thin radial walls — in the cells of the endodermis as many as four such walls were found. The wall of each of the original endodermal cells is in its whole circumference furnished with a cuticularized layer, but as in the exodermis, the thin radial walls which had developed later, were not cuticularised here either. The root was 3-rayed; in transverse section the xylem-part now formed a circular bundle, consisting of vessels and wood-fibres, since the cambium had commenced its activity all the way round. The epidermis evidently dies away very early; even in a root hardly 0.5 mm in thickness, the epidermal cells were found in a collapsed condition.

The root of 5 millimetres thickness, with which the individual from West Greenland, mentioned above, was fur-

nished, had a xylem-cylinder, 3 mm thick, which consisted for the most part of vessels, thin-walled and rather wide; in addition thin-walled wood-fibres occurred.

Parenchyma rays did not occur, neither were there any indication of growth-zones. In the secondary cortex sieve-tubes were rather scantily present. Cork was not developed. In the roots both the endodermal and the exordermal cells were full of a brown substance.

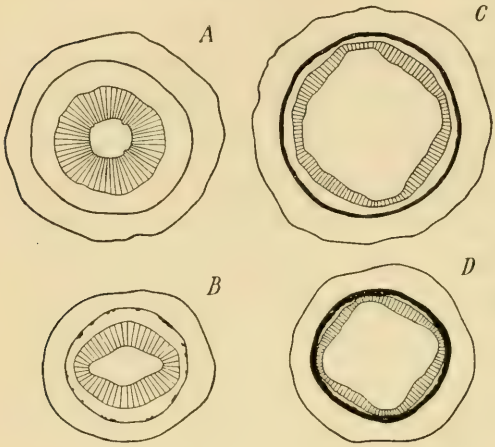

Fig. 17. *Bartschia alpina.* Diagrammatic transverse sections of the stem: *A* and *B*, from runners; *C*, from the aerial stem taken between the 3rd and 4th pair of foliage-leaves; *D*, taken at the point of transition between rhizome and the aerial stem (the black ring in *C* and *D* is the hard-bast, whilst the wood-ring in all the figures is radially shaded). (About $^{18}/_{1}$.)

The Stem. In Hovelaque's work it is particularly the anatomy of the stem which has been exhaustively treated, and *Bartschia* has, on this point, since been again investigated by Hollstein. To this I have nothing new to add, and can therefore confine myself to the following brief description.

A section taken from a little above the middle of the foliage-leaf-bearing part of the stem (a diagrammatic representation is given in Fig. 17, *C*) shows a thin-walled epidermis, beneath which there is a cortex, the outermost layer of which has somewhat thickened cell-walls; several of the cortical cells have undergone division by means of thin radial

walls. In the endodermis — contrary to Hovelaque, who mentions its cells as being "sans cadres" — I found distinct, although rather faint, Casparian dots. The outermost layers of the stele consist here of rather thin-walled lignified prosenchymatous cells; the sieve-tissue forms a continuous ring outside the xylem-part, which in the whole extent of its periphery consists almost exclusively of wood-fibres. The pith consists of thin-walled cells which collapse early in the centre of the stem.

A section taken at about the middle of the subterranean part of the axis, is distinguished from the above by having a more distinct endodermis, the cells of which have, as in the root, a suberised lamella in the whole circumference of the wall — the contents of the endodermal cells have a brown colour —, by entirely wanting hard bast, or at any rate, by having it only in a far more slightly developed degree (in the two diagrammatic figures, Fig. 17, *A* and *B*, the line between the outer edge of the xylem-ring and the periphery is the endodermis, the black dots within this, in Fig. *B*, are small groups of hard-bast cells — in *A* these are totally wanting), and lastly, by a comparatively narrower pith and broader xylem-ring, in which wood-fibres are less numerous and thin-walled.

At the point of transition between rhizome and the aërial stem, the hard-bast appears successively (the cells of the hard-bast are here somewhat more thick-walled than at the top of the shoot), the pith widens, the xylem-ring becomes thinner and richer in wood-fibres throughout its periphery. The sieve-tissue is divided into four larger groups, since the hard bast and the wood-fibres of the xylem-ring at four points which decussate, tend to approach one another, and may practically coalesce at these points (this phenomenon is connected with the passing-out of the leaf-trace-bundles

from the stele, compare Fig. 17, *D*, which is a diagrammatic representation of a part like the one just described — the section was taken between the uppermost scale-leaf and the first pair of foliage-leaves), small groups of sieve-tissue

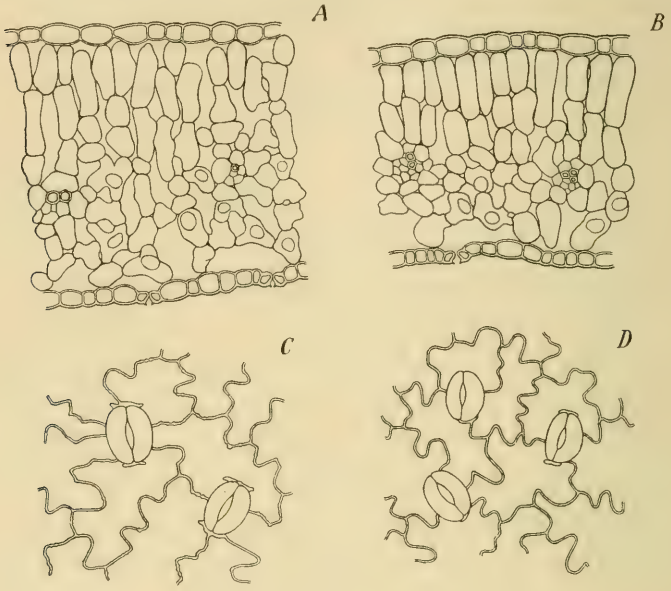

Fig. 18. *Bartschia alpina.*
A and *B*, Transverse sections of foliage-leaves. *C* and *D*, Portions of the epidermis of the upper and of the lower surface respectively. (West Greenland.) (*A* and *B*, about $^{140}/_{1}$; *C* and *D*, about $^{220}/_{1}$.)

elements, however, are always found enclosed in the stereom (well-illustrated in Hovelaque's Fig. 334, p. 405).

Medullary rays do not occur. The epidermis of the rhizome persists for a long time; cork is not developed (Hollstein); in the older rhizomes a successive dying-away of the outer layers of the cortex takes place.

The Leaf. The epidermal cells of both the upper and the lower surface have undulating lateral walls, this being somewhat more strongly the case with those of the lower surface than with those of the upper (Fig. 18, *C* and *D*).

Stomata occur on both leaf-surfaces, but they are more numerous on the lower surface; the proportion between the number of stomata on both surfaces proved to be about 1 to 2. On the upper surface the lateral walls of the epidermal cells are slightly porose, especially near stomata; the guard-cells are surrounded by 3—6 cells, and are on a level with the surface, or project slightly (Fig. 18, *A* and *B*).

The transverse section (Fig. 18, *A* and *B*) shows 1—3 palisade-layers. Both *A* and *B* were drawn from sections of leaves taken from specimens from West Greenland, and in both cases the leaves were chosen from the middle of the stem. *A* is seen to be somewhat thicker than *B*, and to have an assimilatory tissue consisting of as many as 3 cell-layers, the elements of this tissue are somewhat irregular and some of them are slightly branched; *B* probably represents the more common type. The transverse section of the leaves of the Norwegian plants resembles, on the whole, the transverse section shown in *B*, with the exception that the palisade-cells are slightly higher. The spongy parenchyma consists of rather copiously-branched cells. In the palisade-tissue and spongy parenchyma chlorophyll-grains are present in abundance.

The leaves are rather densely covered with hairs; the following types of hair occur: —

(1) Non-glandular hairs, with one or many cells, thin-walled, glabrous and pointed (Fig. 19, *C* and *E*); (2) Glandular hairs with longer, two- or many-celled stalk and a 2—4 celled head (Fig. 19, *A*, *B* and *D*); (3) Glandular hairs with short, one-celled stalk and 2 or commonly 4-celled head (Fig. 19, *F*); (4) Glandular hairs of the kind illustrated in Fig. 19, *G*, *H*, *I* and *K* with a low somewhat sunken stalk-cell, and a cupola-like extremely thin-walled 4-celled head.

By comparision of the figures in question with Fig. 14

C, *D* and *E*, it becomes evident, that this form of glands in *Bartschia* — as already pointed out by Heinricher (cf. his addition to the cited paper of Scherffel) — belongs to the *Lathraea*-type like the similar ones in *Euphrasia*. Fig. 19, *I* and *K* show these glandular hairs seen from above;

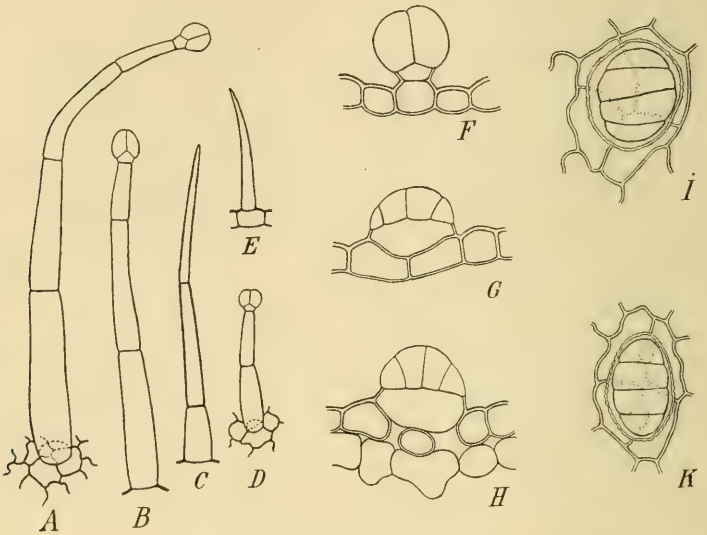

Fig. 19. *Bartschia alpina.*
Different types of non-glandular and glandular hairs from the leaf. (*A*—*E*, about $^{90}/_{1}$; *F*—*K*, about $^{290}/_{1}$.)

below the stalk-cell the lateral walls of the epidermal cells are indicated by dots, in *K* two intercellular spaces are formed between them, 2—4 of these are found rather commonly under the hairs. A glandular hair, similar to that which is seen from above in *K*, is shown in *H* in transverse section, here also 2 intercellular spaces are distinctly seen. *G* and *I* have no intercellular spaces of this kind. Glandular hairs of type 4 occur only on the lower surface of the leaf, under the branches of the veins of higher order; in the same place there is found in addition to this a great number of hair

of type 3, but the latter kind of hair is also found on the upper surface of the leaf, located at the margin of the leaf in the innermost part of its indentations, i. e. above the extreme points of the veins (cf. Fig. 15, *B*). The non-glandular hairs and the long-stalked glandular hairs occur on both leaf-surfaces, and they grow most densely near or upon the veins.

Upon the scale-leaves at the base of the shoots glandular hairs of the type shown in Fig. 19, *F* predominate, they are especially numerous on the lower surface, where the majority of them are found arranged in two broad stripes, one along each of the margins of the leaf; mingled with them are found glandular hairs of type 4.

The stems are covered with multicellular non-glandular hairs, and glandular hairs which frequently have multicellular stalks.

Pedicularis lapponica L.

Alcohol-material from Norway (Aursunden, leg. Th. R. Resvoll, 8. 8. 1918; Skâdavara in West Finmark, leg. E. Warming, 7. 7. 1885).

Herbarium-material from West and East Greenland, *Lapponia murmanica*, Nova Zembla, Labrador, Arctic Siberia and the coast of Hudson Bay.

Lit.: Axell, 1869, p. 102; Lange, 1871, pp. 256 and 265, tab. III, fig. 16 (the seed); 1880, p. 74; 1887, p. 262; Warming, 1886, pp. 44 and 47; 1888, pp. 35, 39, 59 and 87; 1890, pp. 207, 208, 210, 211 and 219; Lindman, 1887, p. 84; Rosenvinge, 1892, p. 686; 1896 (I), p. 68; 1896 (II), p. 78; Hartz, 1894, pp. 37 and 39; 1895 (I), pp. 137, 175, 219, 271 and 288; 1895 (II), pp. 335, 359 and 372; Hartz and Kruuse, 1911, pp. 347, 359, 365, 388, 409, 419, 423 and 428; Ekstam, 1897, pp. 119, 167 and 168; Kruuse, 1898, pp. 373, 380 and 394; 1905, p. 175; Abromeit, 1899, p. 42; Knuth, 1899, p. 190; Dusén, 1901, p. 39; Norman, 1901, p. 457; Cleve, 1901, pp. 9, 39, 57, 70, 71, 76 and 89; Skottsberg, 1901, p. 8; Porsild, 1902, pp. 114, 167, 175 and 187; 1910, pp. 267 and 271; 1912, pp. 382 and 387; 1920,

p. 142; Poppius, 1903, p. 48; Sylvén, 1905, p. 88; Silén, 1906, p. 92; Simmons, 1906, p. 34.

Hemicrytophyte, with a primary root which dies away rather quickly; it spreads by means of slender, subterranean runners. As a rule, these are monopodial: their short vertical portion bears leaf-rosettes, usually through a limited number of growth-periods (1—3), the floral shoots arising as lateral axes on the rosette-axis.

As shown in Fig. 20, *A* and *B* the horizontal portion of the runners has elongated internodes, with small scale-leaves; in the axils of these, buds are formed which grow out into new runners. New runners arise only in the horizontal portion of the parent-shoot. The runners are provided with adventitious roots, which must be described as "restricted to one position only", inasmuch as they arise in connection with the axils of the scale-leaves, as a rule one at each. Haustoria were found on the roots.

When the runner bends upwards, its internodes become short, and the scale-leaves pass without intermediate forms, into long-stalked foliage-leaves, of which it bears 3—7 in the first year (at *x* in Fig. 20, *A* and *B* the dead stalks of the rosette-leaves of the previous year are seen); at the end of the season of growth a number of scale-leaves are again formed, which function as bud-scales for the winter-bud. Some runners pass over directly into their winter-rest, without having succeeded in forming leaf-rosettes in the first year.

Both the scale-leaves under the rosettes, and the rosette-leaves, as well as the scales of the winter-bud, can subtend buds (Fig. 20, *A*, *B* and *D*); the lowermost buds must probably be regarded as reserve-buds; any true principal bud does not occur.

At the beginning of the next season of growth, one or several — as many as 3 — of the buds can grow out into

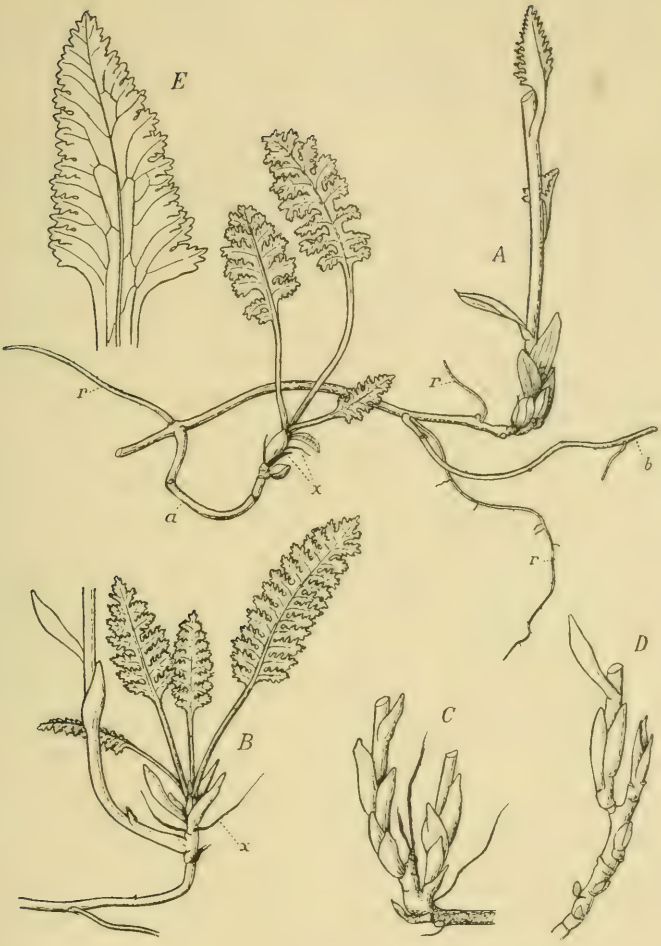

Fig. 20. *Pedicularis lapponica.*

A, A part of a flowering plant. On the runner two new runners (*a* and *b*) have developed as lateral shoots, and an erect, floral shoot, of which only the lower half has been figured; *r*, adventitious roots. The uppermost of the two buds seen just below the floral shoot is the terminal bud of the runner. The runner *a* is in its second year of growth: the withered remains of the rosette-leaves (*x*) of the previous year are seen under the scales of the winter-bud. *B*, The apex of a runner; under the leaf-rosette one sees the scales of the winter-bud, — which scales subtend small buds, — and the withered remains of the foliage-leaves (*x*) of the previous year; a floral lateral shoot has been developed. *C* and *D*, Apices of two runners; *C* with dead, terminal bud

and two lateral shoots (floral), *D* with a floral lateral shoot and four reserve-buds. *E*, One of the leaves of a floral shoot. (*A* and *E*, Greenland.) *A* and *B* about nat. size; *C* and *D* about $^1/_3$; *E* about $^3/_1$. (*B*, *C* and *D* are drawn from sketches by E. Warming.)

floral shoots; as shown in the figures, they bear scale-leaves (*ex parte* bud-scales) at their base; these pass gradually into foliage-leaves in the middle of the shoot. The foliage-leaves of the floral axes differ somewhat in form from the rosette-leaves; the midrib is broader, and the incisions of the margin are less deep (Fig. 20, *E*). The inflorescence is a crowded, almost capitulate raceme, without a terminal flower; according to Warming, the flowers in the middle of the inflorescence, are the first to expand. The terminal bud of the runner, as a rule, continues its growth by forming a second leaf-rosette; exceptionally, it may produce a floral shoot, which consequently becomes terminal; the latter has only scale-leaves at its base. In addition I must remark, that in a single case, I found a runner which, without a previous vegetative-stage (leaf-rosette), terminated directly in an inflorescence.

A runner hardly ever forms leaf-rosettes for more than 3 successive growth-periods. Also in the axils of the scale-leaves of the floral shoots buds occur; in cases in which these develop further, they frequently form, in the following year, shoots of similar structure to the parent-shoot. Warming mentions that at the base of the floral shoots also, rosettes of foliage-leaves may be produced; in some cases I succeeded in demonstrating such leaf-rosettes, but they are evidently of rare occurrence.

The structure and biology of the flower are explained by Lindman and E. Warming, of whose descriptions the following is an extract: The lower lip of the almost horizontally projecting flower incline very decidedly to the right

(seen from the front); besides this, the whole flower is subject to torsion around its axis to the right; this causes the upper lip to slope even more to the right, while its helmet-shaped apex, and the part of the style turned downwards, point to the left; the lower lip stands almost in the vertical plane (Lindman, p. 84, Pl. IV, fig. 47, *A* and *B*).

"The calyx is dark-red, the corolla pale yellow or brimstone-coloured. On the lower lip there are two conspicuous convexities covered with hairs, the corolla-tube is 6—8 mm long" . . . "The slit of the upper lip is about 1—1½ mm wide; the front stamens are slightly hairy or glabrous. The style may be enclosed (and this is the case at the same time as the anthers are open), but usually it protrudes more or less, from 1.5 to 2.5 mm or even more (without being moved away from its natural position up to the dorsal side of the upper lip). Even in the bud it protrudes somewhat, so that the stigma comes into contact with the lower lip; the former is even at that time papillose, and appears ripe, consequently, slight protogyny appears to prevail. Afterwards the anthers are seen to have dehisced, without the length of the style having altered; consequently, self-pollination appears to be able to take place, but not easily, because although it is true that the anthers come to stand vertically above the stigma, yet the distance between them is comparatively great". (Warming, p. 219, fig. 33, reproduced here as Fig. 21).

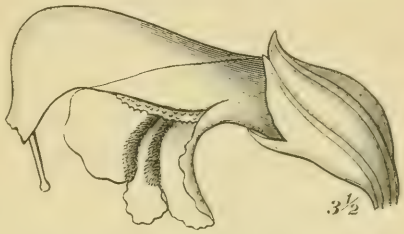

Fig. 21. *Pedicularis lapponica.* A flower with a far-protruding style. (Greenland, about 67° N. lat.) (E. Warming, 1890.)

All authors join in attributing perfume to the flowers of *P. lapponica*; Lindman mentions its "strong perfume",

and Hartz (1895 (I), p. 271) writes, that *P. lapponica* and *Viscaria* filled the air with perfume (East Greenland, 7.7.92).

Pollination takes place by the agency of humble-bees, which, according to Lindman, alight on the upwardly turned, left side of the lower lip; the stigma is consequently, by the torsion described above, turned towards the visitor. According to the same author, the humble-bee thrusts its proboscis into the flower, at the widest part of the slit of the upper lip, at about the middle of it, just above the revolute portion of the edge of the upper lip, but not into the narrow groove between the two convexities of the lower lip.

Several of the specimens from West Greenland had one-year-old fruits, from East Greenland I saw fruit-bearing specimens from Danmarks Ø (N. Hartz leg.).

According to Porsild (*in litt.*) visits of humble-bees are rare, and fruit-setting (in contradistinction to the other *Pedicularis* spp.) is generally not good; many of the capsules are empty, and in others only a few seeds are found. Ekstam's observations from Nova Zembla agree with those of Porsild.

A description and beautiful illustration (Pl. III, Fig. 16) of the seed is found in Lange, 1870.

P. Lapponica is a decidedly middle-summer-flowering species.

Geographical Distribution: Greenland, Arctic America, Labrador, Kamschatka, Arctic Siberia, Nova Zembla, Arctic Russia, Scandinavia and Lapland. Rosenvinge (1892) records, that in West Greenland it is rather common north of 64° N. lat., but very rare south of this. "The northern limit in West Greenland is still unknown, in the fjords at 72°23′ it was so commonly distributed that the northern limit hardly can be here" (Porsild, 1920). In East Greenland the species is only found between 69°25′ and 73°10′ N. lat. (Kruuse, 1905, p. 175).

Habitat: In Greenland it grows in mossy bogs, and in damp places on heaths; the runners creep in the moss, or in slightly decomposed vegetable matter (M. Porsild, *in litt.*); it is "covered by thick layers of snow during winter" (Porsild, 1920). Warming, 1888, mentions it as inhabiting willow copses, herb-slopes and heaths. On Nova Zembla Ekstam found it growing in dry localities, which were exposed to strong insolation. A. Cleve finds it on mountain heights in Lule Lappmark, avoiding wet ground and the poorest heath; she writes: "Sie gedeiht am besten in den Waldregionen und sucht im Hochgebirge relativ trockene Standorte auf, was schon Wahlenberg aufgefallen war."

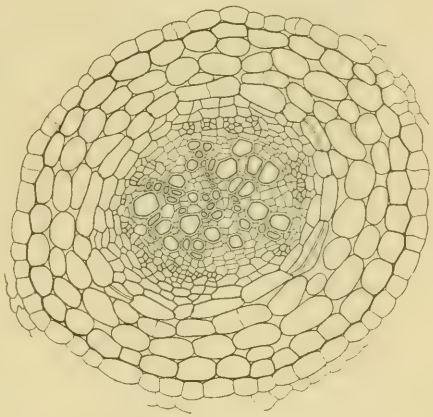

Fig. 22. *Pedicularis lapponica.* Transverse section of an adventitious root (about $^{110}/_{1}$).

Anatomy. The Root: The structure is shown in the transverse section figured in Fig. 22. The secondary growth is not considerable, and does not greatly exceed what is shown in the figure in question. The endodermis is a very beautifully developed Casparian sheath. The epidermis dies away quickly; the outer walls of the exodermis were found to be cuticularised. On the surface of the roots, dark-coloured, fungal hyphæ were frequently found.

The Stem: (1) Runners: The epidermal cells have fairly thick outer walls; they are filled with a homogeneous brown mass, which gave the reaction of tannin. The outermost cortical layer adjoins the epidermis without inter-

cellular spaces; the cells of the cortex show radial divisions by thin walls of secondary formation. The endodermis is exactly as in the root. The pericycle is 4—7 layered, its cells, like those of the cortex, have somewhat thickened walls. The wood-cylinder is continuous, without parenchyma-rays, but is often somewhat excentrically developed, so that the wood on that side of the shoots which is turned down-

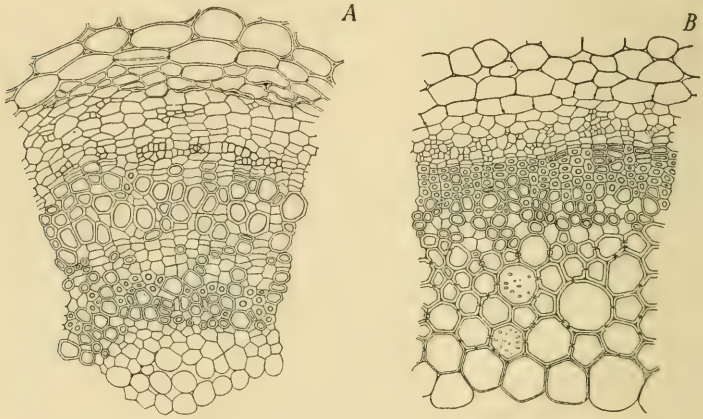

Fig. 23. *Pedicularis lapponica.*
A, Portion of transverse section of runner. *B*, Portion of transverse section of flower-bearing stem. (Greenland.) (About $^{140}/_{1}$.)

wards, is thinner than on the upturned side. As shown in Fig. 23, *A*, annual rings can be formed in the runners. The two annual rings are separated by thin-walled parenchyma, mixed with small vessels, and the vessels are much larger in the second than in the first annual ring. Some stereom (wood-fibres) is seen, especially in the inner annual ring.

(2) The Flower-bearing stem (Fig. 23, *B*) differs from the runners in that the cells of its cortex and of its only 1—2 layered pericycle, are much thinner-walled than in the runners, moreover, by the Casparian spots in the endodermis being much fainter, by the narrower vessels of the xylem-

ring, and the almost continuous ring of wood-fibres on the outer side of the latter, and by the outer layers of cells of the pith being thickened and lignified. The central part of the pith has died away, and the stem is consequently hollow. Stomata occur in the thick-walled epidermis, and chloro-

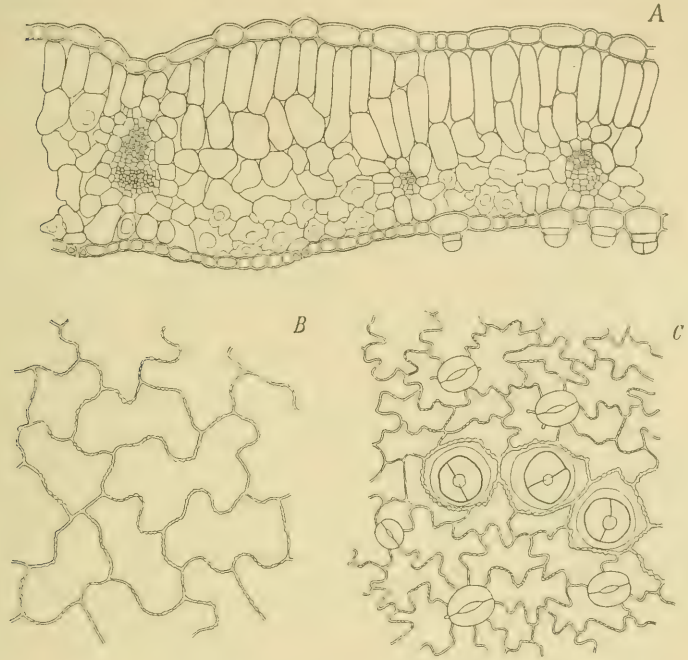

Fig. 24. *Pedicularis lapponica.*
A, Transverse section of the leaf. *B*, Epidermis of the upper, and *C* of the lower surface of the leaf. (Greenland.) (*A* about $^{110}/_{1}$; *B* and *C* about $^{220}/_{1}$.)

phyll in the cortical cells. In the cases in which the basal portions of the flowering-shoots persist and bear lateral shoots, a second growth-ring — often excentric — may be formed here.

The Leaf: As regards the anatomy, there appears to be very little difference between the rosette-leaves and the leaves of the floral shoots. The epidermis of the upper surface (Fig. 24, *B*) has straight to slightly undulating lateral

walls; those of the epidermis of the lower surface (Fig. 24, *C*) are more strongly undulating. The lateral walls of the epidermal cells of both the upper and lower surface, although thin, are yet very distinctly porose, those of the upper surface, more strongly so. Stomata occur only upon the lower surface, the guard-cells are surrounded by 4—6 cells. In transverse section (Fig. 24, *A*) 1—2 layers of palisade-cells are seen; the spongy parenchyma is composed of highly-branched cells (the small circles inside the cells of the spongy parenchyma indicate the branches which have been cut through on preparing the section); chlorophyll-grains are present abundantly in the whole of the mesophyll, also in the epidermis of the lower surface; the stomata occur on a level with, or are raised slightly above, the leaf-surface. The final branchings of the veins end in an epithema-like tissue of somewhat inflated, thin-walled tracheids.

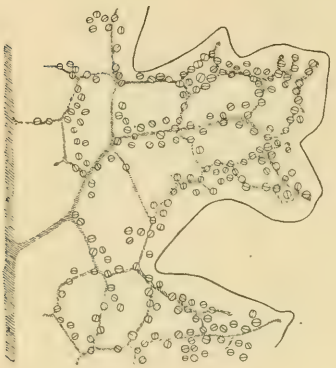

Fig. 25. *Pedicularis lapponica.* A portion of a leaf-section seen from the lower surface; the glandular hairs are seen to be crowded under the veins (about $^{35}/_{1}$).

Very characteristic of the leaves of the *Pedicularis* spp. are the numerous glandular hairs of the type shown in Fig. 24, *A* and *C*. Fig. 25 shows a portion of a leaf-section seen from the lower surface, — the glandular hairs are found here only —, the veins are drawn as if visible through the mesophyll, and the glandular hairs are seen to be crowded under the veins, the same feature is recorded by Hovelacque (l. c.) in the case of other species of *Pedicularis*. In Fig. 24, *C* three glandular hairs are seen from above; the epidermal

cells from which they have developed, have far thicker and more highly porose lateral walls than the surrounding cells; the finely-drawn circle which surrounds the thickly-drawn glandular-head, indicates the place of contact between the basal cell of the hair, and the outer wall of the epidermal cell; the smaller circle at the top of the head indicates that the cuticle at this place is lacking, thus forming a pore only spanned by the cellulose wall, as described by Percy Groom for *P. palustris*.

Pedicularis sudetica Willd.

Herbarium-material from the shore of Hudson Bay (Churchill), King Point, King William's Land, Southhampton Island, Port Clarence, Taimyr Peninsula, Chabarowa, Nova Zembla and Lapland.

Lit.: Lange, 1880, p. 75; Kjellman, 1882 (I), p. 256; 1882 (II), p. 325; 1882 (III), pp. 361, 363 and 366; 1882 (IV), p. 509; Kjellman and Lundström, 1882, p. 303; Holm, 1885, p. 43, tab. VI, fig. 10, tab. VII, figs. 1—7; Warming, 1890, pp. 207 and 215; Ekstam, 1897, pp. 118, 166, 168, 176 and 180; Knuth, 1899, p. 191; Simmons, 1913, pp. 123 and 138.

Sympodial hemicryptophyte of semi or entirely rosette type, the above-ground part of the shoot bearing the inflorescence being either furnished with a few foliage-leaves, or being totally devoid of them.

The species may form tufts, (a specimen from Herschell Island belonging to forma *lanata* Walpers, had numerous rosettes of foliage-leaves, even seven flowering shoots and 10 withered peduncles from previous years) and in this case it has a short mesocorme ("rhizoma multiceps"), a fairly thick primary root, sometimes probably of long duration, adventitious roots being only few in number, but rather vigorous; more frequently it appears, however, that the basal portion of the main shoot dies away, perhaps even

after the first flowering period; the main root is then less vigorously developed, and slender adventitious roots, also from the rhizome-portions of the innovation shoots, are abundantly developed, a circumstance which permits those shoots to continue their existence as independent individuals, after isolation from the main shoot — consequently, the species can be propagated vegetatively (cf. Ekstam).

This difference in the growth is probably conditioned by the nature of the habitat; the tufted individuals must be assumed to have grown on drier soil, while the other form must have lived in damper localities; the fact of my having found *Sphagnum* in connection with the rhizomes of many specimens of the latter type, indicates moist moss-tufts as their habitats.

As regards the duration of the first vegetative stage, it is not possible for me to state anything with certainty, owing to want of material; in a comparatively weakly-developed individual, I estimated its extent as three years.

Fig. 26, *1* shows an individual produced from an isolated innovation shoot; (the figure has been drawn from soaked herbarium-material, and is somewhat diagrammatic). At the base of the relatively-main axis, we see the separation surface (scar) along which it has loosened itself from the parent-shoot; during its first year, the shoot has formed a few-leaved rosette of foliage-leaves, and completed the year's growth by the formation of scale-leaves, for the protection of the winter-bud; (at *I* some fragments of the first year's leaves are seen; the bud *A* is dead). Next year a piece of stem, about 1 cm long and only bearing 2 leaves, was first produced, next a rosette of foliage-leaves, followed in turn by scale-leaves, of which three still remain (two only can be seen). The process is repeated in the following (3rd) year, and simultaneously the buds *C* and *D* in the axils of the

scale-leaves of the 2nd year, expand and produce a few foliage-leaves, some of which still remain in a withered condition (c_1 and d_1 respectively). In the fourth year the individual at last flowered; *IV* indicates the lower portion of the peduncle. *C* and *D* which, like the terminal bud of the shoot,

Fig. 26. *Pedicularis sudetica.*
1, Basal portion of a plant, somewhat diagrammatic; as regards the explanation of letters and numbers cf. text on pp. 432—434. *2*, A flower seen in side view. *3*, The upper lip seen in side view; the reciprocal position of the anthers and pistil is indicated. *4*, Stigma, more highly magnified. (Nova Zembla.) (*1* about nat. size; *2* and *3* about $^3/_1$; *4* about $^{50}/_1$.)

have been protected during the winter-rest by scale-leaves, are forming their second leaf-rosette, the leaves of which are indicated by c_2 and d_2 respectively; and *B*, which rested during the previous summer, has now developed a foliage-leaf, b_2;

the now dead leaves *x* and *y* are from the leaf-rosette formed the year before the main shoot flowered; from the axil of one of the uppermost bud-scales, an innovation shoot *E* has also been developed, and is expanding its first two foliage-leaves.

Here, consequently, the vegetative-stage has lasted 3 years, and this appears to be the rule in individuals of this type; in the tuft-forming type in which, in dried material, this question is far more difficult to decide, it appears to me that the vegetative stage can be restricted to two years.

It still remains to be noted that, although the majority of the individuals which result from isolated innovation shoots, had elongated internodes inserted between the rosettes, yet only rarely were they as long as is shown in Fig. 26, *1*; the phenomenon is probably due to the endeavour of the plant to keep its terminal bud in a certain position relative to the surface of the substratum. In Fig. 26, *1* adventitious roots are developed only at the base of the shoot, but these may also be developed below the other rosettes, often in great numbers. They are 1—2 mm thick. I never found haustoria on such adventitious roots, but they occurred on the root-branches in the specimen from Herschell Island, mentioned above.

From Nova Zembla plants were to hand of which the peduncle was only 5 cm high during flowering; in specimens from Chabarowa it was 17 cm, and in one from Churchill, even 25 cm high; after flowering an elongation of the axis of the inflorescence takes place.

Fig. 26, *2* shows a flower seen from the side. The position of the stigma should be noted, and the two pointed lobes in which the front part of the helmet terminates, and the ridge, with the veins which proceed from it into the helmet, also the slightly warty revolute portion of the edge of the upper lip, and the two convexities on the lower lip;

as stated by E. Warming, the latter is somewhat oblique. The calyx is drawn as densely hairy, this is the case in forma *lanata* Walpers. In Fig. 26, *3* the position of the stamens inside the helmet is shown. It must be borne in mind that the natural position of the flower is almost horizontal, whence it follows that self-pollination must be able to take place with comparative ease, for the pollen will be sprinkled out of the front opening of the helmet by accidental movements of the plant, caused for instance by the wind, and will fall upon the hinder side of the stigma, which, as shown in Fig. 26, *4* is almost globular.

Ekstam has studied the species in Nova Zembla, and he writes concerning this: "Ziemlich häufig — häufig an besonders nassen Orten. Besitzt einen ziemlich starken jasminähnlichen Wohlgeruch und hell- bis dunkelrote Blüten. Schon in sehr jungen Knospen ragt die Narbe aus der Oberlippe hervor — in einer ganz aufgeblühten Blume etwa $2^1/_2$—3 mm — und wird bald papillös, gewöhnlich bevor die Blume ganz aufgeblüht ist, und die Antheren sich geöffnet haben. Selbstbestäubung dürfte dadurch ermöglicht werden, dass die kugeliche Narbe rund umher papillös ist, und in der Falllinie der Pollenkörner gelegen ist. Nachdem die Antheren sich entstaubt haben, bleibt die Narbe noch eine Zeit lang glänzend, papillös. Blüth im Hochsommer. Mit reifen Früchten beobachtet. Anemophile Samenverbreitung. . . . . Wurde am $^{31}/_7$ von einer kleinen Fliege, am $^6/_8$ von einem grossen Bombus hyperboreus Schönh., am $^{18}/_8$ ebenfalls von einem grossen Bombus hyperboreus Schönh. besucht. Im Sommer 1891 trotz fleissiger Beobachtung kein einziger Insektenbesuch bemerkt."

In somewhat vigorous specimens, the exceedingly dense inflorescence, with the deep-red corollas, cannot fail to be very conspicuous.

The Geographical Distribution, according to Simmons and Lange: Western Arctic and Subarctic North America, (both the continent and the archipelago), Arctic Siberia, Nova Zembla, Arctic Russia and besides on mountains

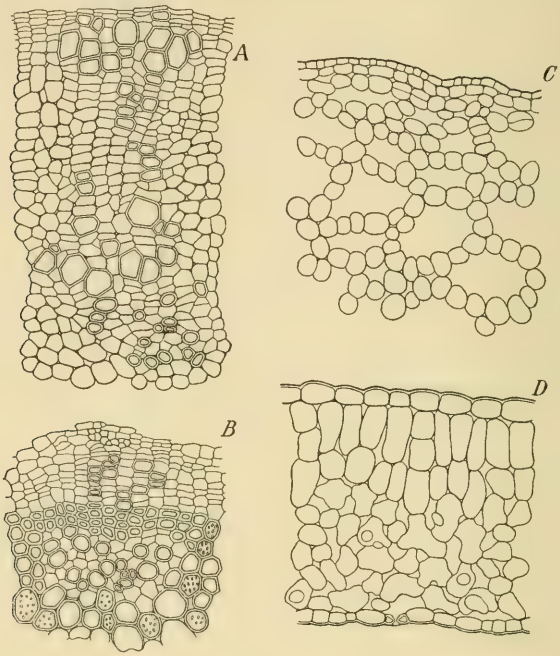

Fig. 27. *Pedicularis sudetica.*
A and *B*, Portions of transverse sections of the rhizome of the individual illustrated in fig 26, *1* (cf. text). *C*, Epidermis and the outer layers of the cortex of the same rhizome. *D*, Transverse section of the leaf. (Nova Zembla.) *A* and *B* about $^{140}/_{3}$; *C* about $^{70}/_{1}$; *D* about $^{110}/_{1}$.)

(Sudeten and Riesengebirge) of Central Europe. Does not occur in Greenland.

According to Kjellman (1882 (III)) the flowering year's-shoots of *P. sudetica* in a pressed and fermented condition, and the roots, rhizomes and buds in fresh condition, are used as food by the Chuckes in Eastern Arctic Siberia.

Anatomy. An adventitious root about 2 mm thick

showed the following structure: Of the exceedingly thin-walled epidermis only scattered fragments were left, the cells were dead and had collapsed. The outermost layer of the cortex had cuticularised outer and lateral walls (it must certainly be this layer which Th. Holm in his Fig. 7, Tab. III, designates epidermis); the layer just within the outermost layer adjoins the latter without or with small intercellular spaces between them; the endodermis has distinct Casparian dots. The intervening part of the cortex consists of a very lacunose tissue, which corresponds exactly with that in the rhizome (shown in Fig. 27, *C*). Such slender adventitious roots complete their development during one season of growth; their structure is 2-rayed, and by the secondary growth there is formed a bundle of xylem-tissue, about 0.5 mm thick consisting of vessels with intervening non-lignified tissue.

Of the individual figured in Fig. 26, *1* a transverse section of the axis was taken from the part between *I* and *II*, and also one between *II* and *III*; the former part must be assumed to be 3 years old, and the latter 2 years. In the part between *I* and *II*, there was found in the stele a circle of vascular bundles, separated by broad, non-lignified, parenchyma-rays (cf. Fig. 27, *A*, which shows the xylem part of a vascular bundle). In the second year of growth an increase of the vascular elements has evidently taken place, the lowermost (i. e. in the stem innermost) group of wide vessels probably indicates the limit of the first year's growth; what is found outside that belongs then to a later (probably the second) year. Wood-fibres are quite absent; here the pith does not die away. Fig. 27, *B* is drawn from a section taken from the part between *II* and *III*, at about the middle of it. Here the axis is hollow, because the central part of the pith, as in the peduncle, has died away; the walls of the outermost layers of the pith have

become thickened, lignified and porose, the same is seen to be the case as regards the inner part of the parenchyma-rays, which separate the vascular bundles. Around the vessels non-lignified elements occur, but the limit of the first-year's growth is shown in the vascular bundles by a layer of wood-fibres, 2—3 cells thick, which adjoins the lignified parenchyma rays, so that a continuous stereom results. The few scattered vessels outside this I regard as the growth of the second year; such small groups of vessels may also occur in the space between any two of the original vascular bundles. A second individual exhibited a similar structure, but in a third I found no trace of a second-year's growth; unfortunately the scantiness of the material prevented my studying this point more thoroughly. A portion of the cortex is shown in Fig. 27, *C*; with the exception of the two outermost layers it is very lacunose in structure. The epidermis is small-celled, and furnished with a rather thick cuticle.

The Leaf. The epidermis is of the usual *Pedicularis*-type, the lateral walls of the cells are thin and only slightly porose, very similar to those in *P. hirsuta* and *lanata*. Stomata occur only on the lower surface of the leaf; the guard-cells are on a level with the other epidermal cells. A transverse section is shown in Fig. 27, *D*; the part which has been illustrated is typical and also agrees well with Th. Holm's Fig. 4, Tab. VII. The upper half of the mesophyll consists of 2—3 layers of short, thick palisade-cells, and the lower half of spongy parenchyma composed of rather decidedly branched cells. Chlorophyll occurs abundantly in the whole of the mesophyll. Glandular hairs of the same form and size as in the other species of *Pedicularis*, occur also in *P. sudetica* on the lower surface of the leaf — not as Th. Holm (l. c. p. 44) writes "here and there," but in abundance below the branches of the veins of tertiary and higher

order. On the lower surface of the leaf, and especially in the middle of the sections, thin-walled 1- to 3-celled non-glandular hairs occur.

Pedicularis euphrasioides Steph.

Alcohol-material from Greenland (Itivnek near Holsteinsborg, leg. Eug. Warming, 13. 7. 1884).

Herbarium-material from Greenland, the shore of Hudson Bay (Churchill), Port Clarence near Behrings Strait, and Siberia (by the Boganida River).

Lit.: Lange, 1871, pp. 254 et seq, 264, tab. II, fig. 10 (the seed); 1880, p. 74; 1887, p. 262; Warming, 1886, pp. 19, 44 and 58; 1890, pp. 206, 210, 211 and 218; Rosenvinge, 1892, p. 686; 1896 (I), p. 68; 1896 (II), p. 78; Hartz, 1894, p. 39; Knuth, 1899, p. 190; Porsild, 1920 p. 142.

Spot-bound hemicryptophyte of the semi-rosette type, biennial to pluriennial hapaxanth, or — what is certainly the most common — a pollacanth, with scantily-branched main root, the longevity of which corresponds with that of the individual. Should the species appear as a pollacanth, innovation shoots are developed at the base of the flowering shoot.

The length of the first vegetative-stage varies from one to (probably at most) two years. During the vegetative stage a leaf-rosette is developed every summer and — towards the end of the growth-period — bud-scales for the protection of the young organs during the winter-rest; in the summer in which the plant flowers, the shoot forms no rosette of foliage-leaves. The shorter vegetative-stage (of one-year's duration) appears especially to result in weaker individuals, which probably often end their lives by fruit-setting in the second year.

This species differs very much in habit from the other species described here, owing to the formation of numerous

branches which, during the flowering year, arise in the axils of the foliage-leaves on that part of the stem which has elongated internodes. These lateral shoots increase in length downwards to some way below the middle of the parent-shoot, and then again become shorter towards its base; here they are often purely vegetative, while the upper ones bear, in addition to 2—3 decussated pairs of foliage-leaves, a small inflorescence corresponding with that of the parent-shoot.

In the pollacanthous individuals the innovation shoots are produced in the axils of the uppermost bud-scales; they usually develop only a few pairs of opposite foliage-leaves, then bud-scales, and then the following year, they most often terminate their growth by the formation of an inflorescence. I cannot deny that there is a possibility of the innovation shoots also flowering without any preceding rosette-formation, and therefore, in their first year, developing only bud-scales; in this case the species would be a transitional form between the semi-rosette type and the protohemicryptophyte-type.

In individuals in which a "rhizoma multiceps" is developed, the uppermost part of the main root may become as much as 2 cm thick.

The flower-bearing stem may become as much as 25 cm high; after flowering, the axis of the inflorescence is somewhat elongated.

On the basis of material from Greenland (about 67° N. lat.) E. Warming gives the following description of the structure of the flower (cf. Fig. 28): "This species, which is in no wise common in Greenland, is very conspicuous owing to its numerous inflorescences with yellow, fragant flowers; the tip and the helmet of the yellow corolla is slightly brownish. The flowers are very oblique, the lower lip being highly oblique (Fig. 28, *A*, *B*, *D* and *H*); but the upper lip also is

twisted in such a manner that its two-toothed tip turns somewhat to the right (*E*). The ridge reaches the edge slightly above the beginning of its revolute portion (*A* and *G*). The slit between the two edges of the upper lip is usually rather narrow. The front filaments are sparingly hairy. The stigma protrudes more or less above the two teeth (*B*, *D*, *E* and *H*).

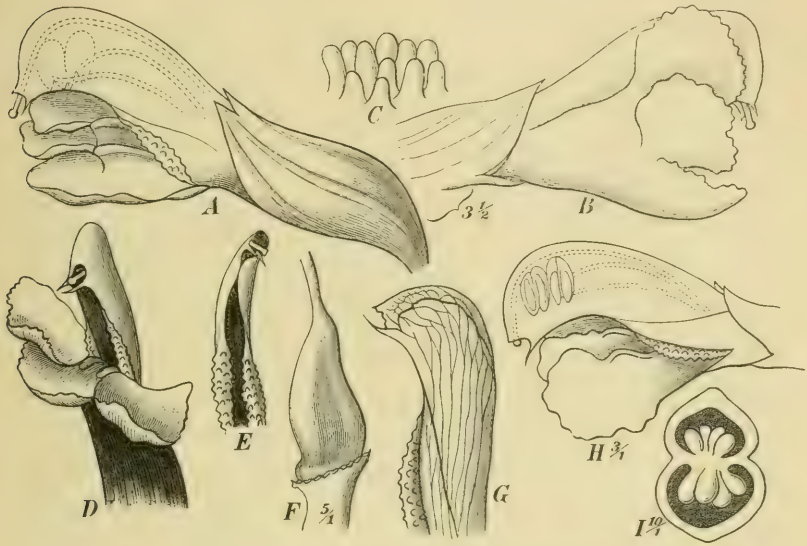

Fig. 28. *Pedicularis euphrasioides.*
(From Greenland; about 67° N. lat.)
A, *B*, A flower seen from the left and the right side; in *A* the position of the style and the stamen is indicated. *C*, Stigmatic papillæ. *D*, A flower in front view. *E*, The upper lip seen in front view. *F*, The ovary. *G*, The upper lip seen in side view; the venation is indicated. *H* shows the same as *A*. *I*, Transverse section of ovary. (Drawn by E. Warming, 1890.)

Judging from the structure of this almost horizontally-placed flower (*A* and *B*), I must assume that it is only with difficulty that it pollinates itself. It produces ripe fruit in Greenland at 67° N. lat."

Geographical Distribution. West Greenland between 62° (but only in a few localities south of 64° N. lat.)

and 69°30′ N. lat. (Rosenvinge, 1892), on the whole rather rare there; Labrador, the Rocky Mountains, the continent of Arctic America, (but not mentioned by Simmons from the Archipelago), Siberia and Dahuria.

In Greenland it grows on luxuriant, damp heaths; the species requires a snow-covering during its winter-rest (M. Porsild, 1920).

Anatomy. The root is of the type described later on in *P. hirsuta* and *lanata* and, as in these, the secondary cortex is traversed by numerous radial clefts. There is, however, a difference between *P. euphrasioides* and the two species in question as regards the nature of the xylem-part, because, in the two former it is composed of a large quantity of non-lignified tissue and of relatively few vessels only, whilst in *P. euphrasioides* one always finds in the root several concentric rings, each consisting of numerous vessels with intervening lignified stereom (thin-walled wood-fibres). These continuous rings of lignified elements, the outlines of which are however somewhat undulating, are separated by portions in which the vessels are not so wide or numerous, and are surrounded by non-lignified tissue; here clefts occur between the radiating lines of vessels.

That these rings of vessels and wood-fibres really indicate zones of annual growths, is evident from the investigation of some specimens chosen from among the individuals in my material, which had flowered for the first time: such as — judging from the leaf-scars — had had only a vegetative-stage of one-year's duration (that is to say, flowered in the second year) showed two rings; others which, as far as I could see, had had a vegetative-stage of two-year's duration, showed three rings. The greatest number I succeeded in demonstrating amounted to three.

The cavity of the stem is comparatively large. The

cortex is thin; in the xylem-ring the wood-fibres dominate in the 3—4 outermost layers; the cell-layers in the periphery of the pith are lignified, thickened and porose. On the epidermis there are found non-glandular hairs of the same type as on the leaves.

The Leaf. A transverse section of one of the leaves

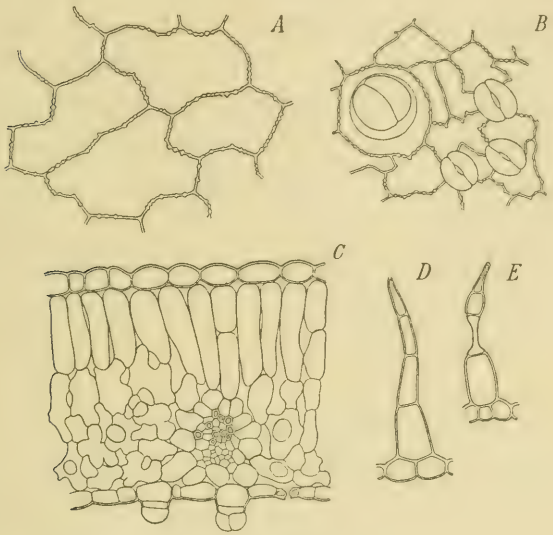

Fig. 29. *Pedicularis euphrasioides.*
A, Epidermis of the upper, and *B* of the lower surface of the leaf. *C*, Transverse section of the leaf. *D* and *E*, Non-glandular hairs from the surface of the leaf. (Greenland.) (*A* and *B* about $^{220}/_{1}$; *C* about $^{110}/_{1}$; *D* and *E* about $^{140}/_{1}$.)

from the middle of the stem, is shown in Fig. 29, *C*. There is generally found only one layer of rather elongated palisade-cells, below these there is usually a layer of cells which, although elongated, are nevertheless branched (this is distinctly seen to the left in Fig. 29, *C*), and which must therefore most naturally be included in the spongy parenchyma; the lower layers of the latter consists of richly-branched cells.

The epidermal cells of the upper surface has thin, slightly

undulating lateral walls, those of the lower surface are still more thinwalled, their lateral walls more highly undulating and, as in the epidermis of the upper surface, furnished with flange-like thickenings, which I found to be particularly well-developed in the bracts of the flowers, and, on the whole, in the upper leaves on the axis. Stomata occur only on the lower surface; the guard-cells are on a level with the other cells of the epidermis; they are surrounded by 3—6 cells. Chlorophyll is abundantly present in the whole of the mesophyll and is also found in the epidermis of the lower surface. On the lower surface there are glandular hairs of the usual kind, and with the typical distribution; and besides there are non-glandular hairs both on the upper and the lower surface (Fig. 29, *D* and *E*); they are multicellular and thick-walled, often however with one or two cells unthickened and therefore collapsed.

Pedicularis Sceptrum carolinum L.

Alcohol material from Aursundsöen, Norway (leg. Th. Resvoll, 11. 8. 1918). — Herbarium material from the district near the river Boganida, Alten, Mortensnæs in East Finmark, and the Murman Coast.

Lit.: Lange, 1871, pp. 254 et seq., 267, tab. III, fig. 25 (the seed); Warming, 1890, p. 215; Norman, 1895, p. 456; Kerner, 1898, Bd. II, p. 655; Knuth, 1899, p. 191; Silén, 1905, p. 92.

A sympodial hemicryptophyte of rosette- or semi-rosette type, with vertical or obliquely-ascending mesocorme, which dies away behind, and from which adventitious roots, 1—2 mm thick, are abundantly developed.

2-year-old specimens, from Aursundsöen, showed that the plant in its first year forms a few-leaved rosette; the winter-bud is protected by scale-leaves, and the following year the growth is continued by the formation of a more

luxuriant rosette. I can state nothing as regards the duration of the first vegetative-stage, the 2-year-old plants in question were still rather frail. The hypocotyl was somewhat elongated, the adventitious roots had already begun to develop, and in one of the individuals, a lateral shoot had been produced in the axil of a rosette-leaf of the first year.

On the rhizomes, innovation-shoots, from 1 to 3 in number, occur; their vegetative stage, judging from the material at my disposal, which is however but scanty, extends over 2 years: During the first year 2—4 foliage-leaves are developed, and then scale-leaves, which serve as bud-scales for the winter-bud; during the next year a somewhat more dense rosette is developed, again succeeded by scale-leaves; and finally the shoot, during the 3rd year, after having formed a luxuriant rosette, terminates in an aerial, flower-bearing portion, which is often quite destitute of foliage-leaves, and may attain a height of even 60 cm.

The fact that the rhizome dies away behind, in conjunction with the abundant development of adventitious roots, must allow of vegetative propagation, since the lateral shoots gradually become free and independent by the dying away of the parent rhizome.

E. Warming (l. c. p. 215 et seq, figs. 30 and 31) gives the following description of the structure and biology of the flower, on the basis of material from Kola, and from Østerdalen in Norway; his two groups of figures are reproduced here as Fig. 30 and Fig. 31.

"The flowers are . . . . as much as 32 mm long; they stand erect, the subtending bracts are closely adpressed, and in addition each flower appears to be completely closed. The lower lip (Fig. *E*) is erect, 14—15 mm long, pressed closely to the upper lip, which is a little longer (16 mm), and closes the throat completely, but is easily pressed down. The visit-

ing insects must evidently be large and vigorous, such as humble bees and moths, and they must, in a way similar to that in *Antirrhinum* and *Linaria*, press their body or head down between the two lips, by which means they primarily come into contact with the stigma; Fig. 30, *B* shows (the lower lip having been removed) that the stigma can be so protruding that contact with it must be regarded as inevit-

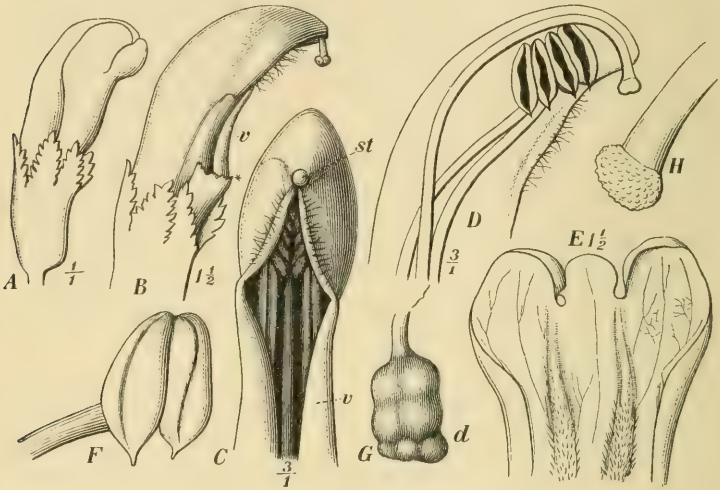

Fig. 30. *Pedicularis Sceptrum carolinum.*
From Kola near the White Sea (collected by Dr. Brotherus). *A*, Flower, natural size and position. *B*, The same after the lower lip has been removed (*D* belongs to this). *C*, Part of a 25 mm long flower, seen in front view; the stigma protrudes less than it does for instance in *B*; the anthers have not yet opened (see *F*); to this belongs the tip of the style shown in *H*. *E*, The lower lip of *B*. *G*, Ovary. *v* indicates the revolute portion of the edge of the upper lip. (E. Warming, 1890.)

able; that cross-pollination must take place by the agency of large insects, is also evident from the fact that the distance from the stigma to the nectary may be as much as 2.5 cm. I have also several times seen the stamens torn off the upper lip, evidently by the violence of a large insect. In one of the flowers (*C*) which has been illustrated, the anthers had

not yet opened (*F*), and as the stigma appears to be ripe (*H*), protogyny must consequently prevail. When the anthers have afterwards opened (*D*) it must evidently be the insect knocking against the filaments, which shakes the pollen down over it; strange to say, both the filaments, anthers, style as well as the revolute portions of the edge of the upper lip, are quite glabrous (see *B*, *C* and *D*) so that there is no special contrivance which by its resistance increases the shock. On the other hand, hairs occur — which are probably of importance in preventing the pollen-grains from falling out at the sides — viz., along the edges of the upper part of the upper lip (*B*, *C*, *D*), consequently, in the same place as ordinarily, but on another organ.

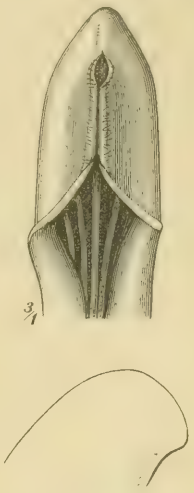

Fig. 31. *Pedicularis Sceptrum carolinum.* From Kola. The upper lip in front and side view. The anthers are open. In the front there is a flat or incurved part, and the slit is tightly closed above. In this case the stigma does not protrude, but stands just within the uppermost end of the slit. (E. Warming, 1890.)

For the rest, the width of the slit of the upper lip, and the degree to which the stigma protrudes, differ also. While the stigma protrudes far out in the quite young flower *B*, it does not protrude so far in the young *C*, and still less in Fig. 31 (also in this paper Fig. 31) of which the anthers are already open . . . . Self-pollination appears to be able to take place only with difficulty. As the species sets fruit abundantly in so northerly a region as near Alten (about 70° N. lat.) it must undoubtedly be humble-bees that effect pollination."

Conditions pertaining to the pollination of the flower

have afterwards been studied by Silén, who writes: "Were much-visited by humble-bees, which forced themselves into the closed flowers, which were thereby torn open on the one side, seen from the front, the right side, whereby the lobes of the lower lip are bent outwards. After the visit of a humble-bee, the flower cannot close again. The smaller humble-bees penetrate entirely into the flowers, whilst the stomach of the larger ones remains visible outside the flower."

In flowers from Aursundsöen I found the lower lip to be relatively somewhat longer than is figured by Warming; the length of the style was, on the whole, the same as that shown in Fig. 30, *B*. Many of the older flowers in the inflorescences had been opened by the visits of insects.

Geographical Distribution: Fennoscandia, Lapland, Western and Northern Russia, Siberia as far eastward as to the river Kolyma, Mantchooria and Japan. Besides this, the species has an area of distribution in Central Europe (Germany, with a southern limit in the Bavarian Alps); here it is possibly a glacial relict (Kerner).

According to Norman, in Northern Norway the species grows in bogs, on boggy plains, on the coast and in willow copses.

Anatomy. The Root. The epidermis remains long intact. The cells in the outermost layer of the cortex are provided with a cuticularised lamella along the whole of their circumference; between this exodermis and epidermis there are no intercellular spaces, and such are wanting also between the exodermis and the outermost layer but one of the cortex; further inwards, the cortex becomes rather lacunose. Starch occurs in the cortical cells. The endodermis is a typical Casparian sheath. When the secondary growth in the stele is completed, a small central group of vessels, circular in outline, is found to be developed.

The Peduncle. A portion of a transverse section is shown in Fig. 32, *A*. The layer of complete cells seen uppermost in the figure, is the endodermis. The pericycle is several-ay ered; sieve-tissue occurs rather sparsely. The vigorous development of the stereom of the peduncle, is characteristic

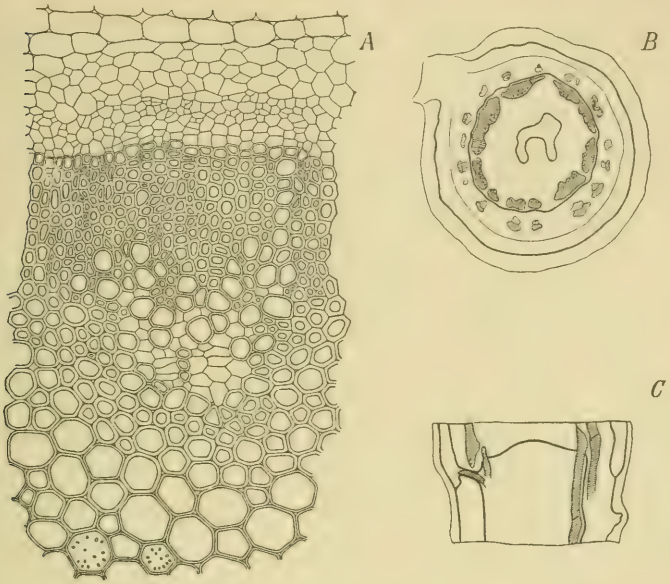

Fig. 32. *Pedicularis Sceptrum carolinum.*
A, Portion of a transverse section of peduncle. *B*, Transverse section, and *C* longitudinal section of the upper part of a rhizome; *B* and *C* diagrammatic, cf. text. (Aursundsöen, Norway.) (*A* about $^{220}/_{1}$; *B* and *C* about $^{6}/_{1}$.)

of the species. In the mass of wood-fibres only here and there a radial row of vessels is inserted — in the figure the 4th row from the right hand is such a radial row. In between the groups of the primarily formed vessels, of which one is seen in the middle of the figure, the wood-fibres internally adjoins the peripheral portion of the pith, which also consists of strongly thickened, lignified and porose cells, so that in the fully developed stem the original groups of vessels are

found completely surrounded by a compact mass of stereom; only the tissue immediately surrounding the protohadrome remains unthickened and unlignified.

The anatomical structure in that portion of the stem which bears the rosette-leaves deserves a more special description.

A transverse section of an axis of an innovation-shoot in its first growth-period, about 3 mm thick, exhibited a distinct Casparian sheath, and in the stele a circle of small vascular bundles, separated by comparatively broad rays of intervening parenchyma; at a depth of about 3—5 layers of cells within the cortex there had been formed, even at that point of time, a cork-cambium which had produced a 3—6 layered cork (Sudan III).

The transverse section of a 2-year-old rhizome, with its richer 2nd year's leaf-rosette developed, exhibited in its uppermost part a structure similar to that described in the case of the one-year-old shoot, only, the diameter of the organ was larger (about 5 mm), the vascular bundles were more numerous and also individually broader, and they had on the outer side of the xylem-portions a thick cap of wood-fibres. In the basal portion of this shoot, which had been developed the year before, and which was consequently 2 years old, there occurred, however, a distinct growth-zone in the vascular bundles, since, either as a direct continuation of the xylem-portion developed during the first year of growth, and furnished on the outer side with a cap of wood-fibres, or else separated from that xylem-portion by 1—3 layers of thin, unlignified elements, one more xylem-portion was found, which also had a cap of wood-fibres along its peripheral portion, and evidently represented the growth of the 2nd year. Frequently, such xylem-groups of the 2nd year are also developed without being in connection with the

xylem-groups of the 1st year, viz., opposite the parenchyma-rays which separate the original vascular bundles. The cork in the primary cortex is constantly few-layered only.

Lastly, a portion of a rhizome of a 3-year-old shoot with a terminal peduncle, was investigated. The basal portion was found to be unaltered, as described above in the case of the 2-year-old shoot; in the part developed during the 2nd year of growth (illustrated diagrammatically in Fig. 32, *B*), fundamentally, the same development has taken place as that which, in the second year, took place in the basal portion, the only differences being that here the vascular groups are larger and more numerous, and the stereom-caps much thicker, and also that the two zones of growth are separated by a ring of non-lignified tissue (parenchyma) as much as 15 cell-layers thick, in which a layer of cork, consisting of 3—5 layers of cells, is developed; this layer of cork surrounds, in a tube-like manner, the xylem developed during the first year of growth. In the figure the cambium is consequently situated immediately outside the outermost circle of xylem-groups; the endodermis is in part distinct, and in the figure, is indicated by a fine line; the two thickly-drawn circles indicate the outer and inner cork-layer; within the pith there is another one like it, also indicated by a thickly-drawn line; in the outer circle of xylem-groups, the inner, dotted part indicates that this part consists especially of vessels, the outer radiately-shaded part, that there wood-fibres predominate, in the inner circle where the situation of the vascular- and stereom-elements is less sharply distinguishable, the whole of the xylem is shaded.

Where the rhizome bears the rosette of the 3rd year, it shows a transition to the structure of the peduncle, and gradually merges evenly into the latter — the wood-fibres form an almost continuous ring, and cork-development ceases.

Fig. 32, *C* shows a diagrammatic, longitudinal section of that portion of the 3-year-old rhizome described above, in which the boundary line between 2nd and 3rd year's growth occurs — here, also, the thickly-drawn lines indicate the cork-layers, and the xylem is shaded. As is evident from

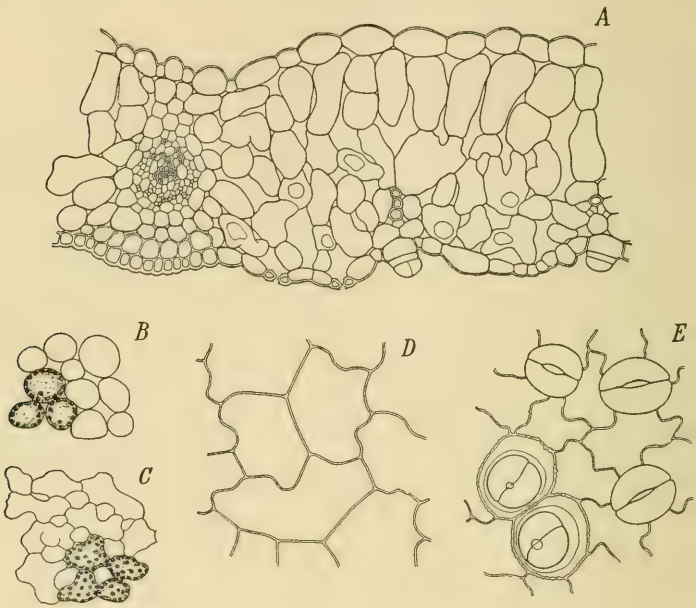

Fig. 33. *Pedicularis Sceptrum carolinum.*
A, Transverse section of leaf. *B*, Palisade cells, and *C*, spongy parenchyma in surface view. *D*, Epidermal cells from the upper, and *E* from the lower surface of the leaf. (*A*, *B* and *C* about $^{110}/_{1}$; *D* and *E* about $^{220}/_{1}$.) (Aursundsöen, Norway.)

the figure the inner layer of cork is continued horizontally in an inward direction, and forms a plate right across the pith; the outer layer of cork shows various irregularities.

A closer investigation of the process of development was not possible, owing to the very scanty material; as regards the development of a continuous layer of cork between the growth-zones of the xylem, it must be noted, that a similar

structure, according to the investigations of L. Koch[1] and E. Strasburger, is found in the aereal stems of *Sedum populifolium* L.

The Leaf. The epidermis of the upper surface has lateral walls, varying from straight to slightly undulating; only along the edges of the sections are the undulations more marked, very much as on the lower surface (Fig. 33, *D* and *E*). The lateral walls are thin, and faintly and distantly porose; only those cells on the lower surface which bear glandular hairs, have, as is also the case in the other species, thicker and more highly porose walls. The transverse section shown in Fig. 33, *A*, exhibits the lacunose structure of the mesophyll: the 1—2 layers of short palisade-cells, which tend to be almost isodiametric, and the usually abundantly-branched cells of the spongy parenchyma; a surface-view of the latter cells is shown in Fig. 33, *C*. Stomata occur only on the lower surface; the guard-cells are on a level with, or project only slightly above, the epidermal cells, which surround them to the number of 4—6. Chlorophyll occurs abundantly in the whole of the mesophyll, and also in the epidermis of the lower surface. Non-glandular hairs are totally absent; glandular hairs of the usual type occur in great numbers under the secondary veins, and the veins of higher order of the leaf-sections.

Pedicularis capitata Adams.

Herbarium-material from St. Lawrence Bay, King William's Land (Gjöa Harbour), Ellesmere Land, Kotzebue Bay, Island of Iglorlik and from near the Taimyr River.

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[1] L. Koch: Untersuchungen über die Entwicklung der Crassulaceen. Heidelberg, 1879, and E. Strasburger: Ueber den Bau und die Verrichtungen der Leitungsbahnen in den Pflanzen. Jena, 1891. pp. 324—326.

Lit.: Lange, 1880, p. 78; 1887, 262; Kjellman, 1882 (I), p. 257; 1882 (IV), p. 511; Rosenvinge, 1892, p. 687; Eastwood, 1902, p. 288; Simmons, 1906, p. 26; 1913, pp. 125 and 139.

A sympodial hemicryptophyte of the rosette-type, which spreads by means of slender runners. The runners bear small scale-leaves and, rather scantily, adventitious roots, which are given off at the nodes; on some of the roots haustoria were found.

The length of the vegetative period of the innovation-shoot varies from 1 to 4 years; during the first year of growth it develops at its apex either a winter-bud only, or it first forms a small rosette of 2—4 leaves. In one single case I found the shoot already flowering in the following year, but as a rule a rosette of foliage-leaves is formed in one, two, (which appears to be the most common), or three more years. The flower-bearing axis is terminal, as much as 9 cm high, most frequently quite leafless, rarely with 1—2 foliage-leaves; at its apex it bears 2—6 flowers in a capitate raceme; some fresh leaves are always found at its base, since the shoot, also in the year in which it flowers, begins the year's growth by the development of a small rosette of foliage-leaves. The winter-buds are protected by scale-leaves.

In that part of the shoots where the leaf-rosettes are developed, branching seldom takes place; the new shoots arise most frequently from the portion of the runner immediately below the rosettes, or from the part of it, where it turns upwards. The runners are as much as 2 mm thick; how long they may become, I am not prepared to state, owing to the scantiness of the material, which would illustrate this point; several runners measured 3—4 cm. Sometimes they may be quite short, or a runner-like portion is entirely lacking at the base of the innovation-shoot, so that several flowering shoots may occur close together.

The structure of the flower is shown in Fig. 34, *A*—*D*; as I had only dried plants at my disposal, these drawings are somewhat diagrammatic.

As in *P. Sceptrum carolinum* the lower lip is directed upwards, on its inner side (morphological upper side) are two convexities. The maximum distance from the base of the corolla-tube to the tip of the helmet, was 3 cm; the

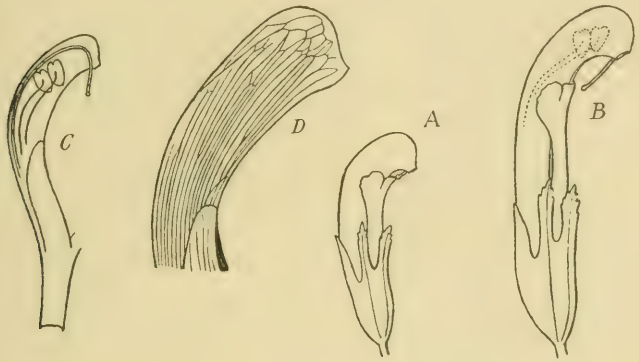

Fig. 34. *Pedicularis capitata.*
A, A bud and *B* a fully expanded flower; in *B* the position of the anthers is indicated. *C*, Corolla-tube and upper lip cut through the median plane of the flower, the lower lip has been removed. *D*, Uppermost half of the upper lip, more highly magnified in order to show the venation of the helmet; lowermost in this figure one sees the uppermost parts of the ridge and of the revolute portion of the edge of the upper lip respectively. (Ellesmere Land.) (*A*, *B* and *C* about $^3/_2$; *D* about $^3/_1$.)

colour of the corolla is yellow. The position of the ridge is shown in Fig. 34, *C*, and the venation of the helmet in Fig. 34, *D*; in the latter figure the uppermost part of the ridge is seen, and a little of the narrow revolute portion of the edge of the upper lip (entirely black in the figure). The revolute portion appears as if it were smooth, but, under the microscope, some of its epidermal cells are seen to be furnished with quite small, warty protuberances with cuticular striations; such protuberances are also found along the

edges of the helmet, above the revolute portion. The corolla-tube is somewhat hairy within, in its lower part.

The length of the style and the position of the stigma varied greatly, even in flowers from the same plant. The relatively longest-styled flower in my material was the one shown in Fig. 34, *B*; the plant to which it belonged came from Ellesmere Land; Fig. 34, *A* shows a not yet open flower from the same plant. From Ellesmere Land I have, however, also had flowers in which the style was so short that it hardly reached outside the tip of the helmet, whilst in others it protruded 1—2 mm outside, but was bent more or less decidedly upwards.

In several specimens from King Point there were flowers in which the end of the style was bent so strongly inwards, that it came to lie within the edges of the helmet, close up to the anthers. Some flowers from the Island of Iglorlik showed that, in the older ones, the point of the style may be bent more inwards than in the younger ones of the inflorescence; anything corresponding to this I have, however, not succeeded in confirming in flowers from the other localities. With the exception of the cases in which the stigma protrudes slightly, self-pollination by falling pollen must easily be able to take place, naturally, more especially where the stigma, is bent close under the anthers.

According to Simmons *P. capitata* flowers on Ellesmere Land at the beginning of July, and in most years does not, in all probability, succeed in setting fruit there, for which reason it will often be under the necessity of reproducing itself vegetatively by means of its runners.

As regards its habitat, Simmons remarks, that the species grows chiefly in marshy soil, but may also be found in drier localities where, however, the inflorescence becomes poorer (1—2 flowered).

According to the same author, the Geographical Distribution of *P. capitata* is as follows: North-western Greenland, Arctic American Archipelago, Arctic America, Unalaschka, East-Arctic Siberia to Taimyr Peninsula, and Kamschatka.

Anatomy. The Root: The structure of evidently full-

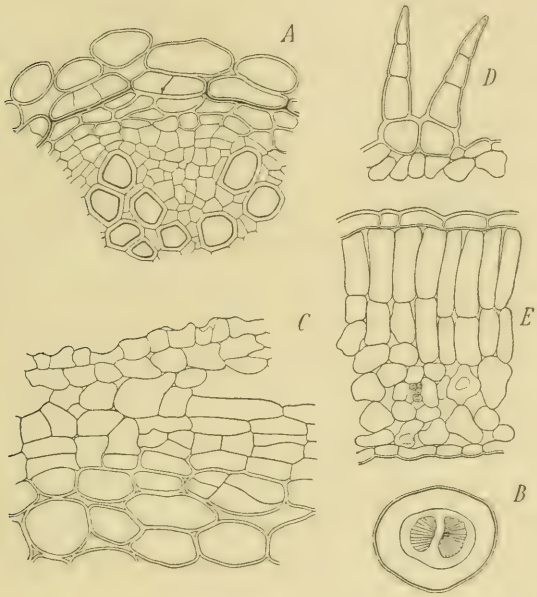

Fig. 35. *Pedicularis capitata.*
A, Portion of a transverse section of root. *B*, Transverse section of a runner, diagrammatic, cf. text. *C*, The peripheral layers of a runner in transverse section, showing the cork-formation. *D*, Two non-glandular hairs from the lower surface of the leaf. *E*, Transverse section of leaf. (*A* and *C* about $^{220}/_{1}$; *B* about $^{16}/_{1}$; *D* about $^{140}/_{1}$; *E* about $^{110}/_{1}$.)

grown adventitious roots, about 0.5 mm thick, was as follows: The epidermis appears to die away rather quickly; the cells in the outermost layer of the cortex have cuticularised outer and lateral walls; the cells under the exodermis were frequently divided by a thin tangential wall. The

cortex is few-layered (5—7 layers), the cells in the 3 outermost layers unite closely without any intercellular spaces; starch is found in the cortical cells.

During the secondary growth of the root, the endodermal cells are elongated tangentially, as are the other elements of the cortex and, are divided as the exodermal cells, by thin radial walls, into 2—4 cells; moreover, in the inner walls, and in the primary radial walls, there is formed a cuticularised lamella (the thickly drawn line in Fig. 35, *A*), so that the stele becomes, so to speak, surrounded by a tube of cuticularised material, only interrupted by non-cuticularised passage-cells opposite to the protohadrome-rays; (the roots investigated were 2—3 rayed). The secondary growth of the root stops when a thin bundle of xylem-tissue, circular in outline, and surrounded by a narrow zone of sieve-elements, is developed in the stele.

The Peduncle presents nothing particular in its anatomy. Chlorophyll-grains are found in the cortical cells, the cells of the outer layer of the cortex have somewhat thickened outer and inner walls; the endodermis has recognizable Casparian dots. In the periphery of the xylem-ring the wood-fibres dominate; the outer layer of the pith has thickened, woody, porose cell-walls; the central cells of the pith are thin-walled and die away. On the surface multicellular non-glandular hairs occur.

On the other hand, the anatomical structure of the runner-like part of the shoots deserves a fuller treatment. A diagrammatic transverse section is shown in Fig. 35, *B*; the thickly drawn line slightly within the periphery indicates a cork-layer, a portion of it is shown in Fig. 35, *C* under higher magnification. The outermost (uppermost) layer of cells in the latter figure, is the epidermis; this, together with the 2—3 outermost layers of the cortex, naturally dies away as

soon as cork-formation commences, yet how early in the development of the runner I am not prepared to state, but it probably happens rather early. The amount of cork developed is small; more than five layers of corky cells (the thin-walled elements placed in radial rows seen in the figure) never occur, in fact, often only 2—3 layers; sometimes the cortical layer situated immediately under the epidermis, forms the cork-cambium. This cork-formation is continued from the runner-like, into the rosette-bearing part of the shoot.

In the stele, which is surrounded by an endodermis of a similar kind as that of the root (in Fig. 35, *B* the innermost circle indicates the endodermis), two groups of xylem are found; the vessels are intermingled with non-lignified parenchyma, and the groups are separated by two broad medullary rays, diametrically opposite to each other, in the outer part of which a small group of narrow vessels occurs (leaf-traces). The pericycle is several-layered; like the cortex, it consists of cells with somewhat thickened walls. In the perifery of the xylem-groups a few wood-fibres sometimes occur.

The Leaf. The epidermis of the upper surface has lateral walls varying from straight to slightly undulating, comparatively thick, but only slightly porose; on the lower surface of the leaf the lateral walls of the epidermal cells are found to be slightly undulating; the cells are essentially more thin-walled than those of the upper surface. Stomata occur only on the lower surface of the leaf; they are surrounded by 4—9 cells.

A transverse section of the leaf is shown in Fig. 35, *E*; as far as I could judge from the material at my disposal, the portion which has been selected for illustration is typical: 2 layers of palisade-cells, and a few-layered spongy parenchyma with cells, which do not, on the whole, branch very copiously, are seen.

On the lower side of the leaf-lobes, glandular hairs of the usual *Pedicularis*-type are found, below the branches of the veins of higher order; the dense covering of non-glandular hairs on the lower surface of the leaf as well as on the leaf-stalk, is very characteristic of the species; the hairs (Fig. 35, *D*) are 2—5-celled, rather thick-walled, pointed and smooth, they are especially numerous below the branches of the veins of lower order, and along the leaf-margin, but are also found scattered here and there among the glandular hairs, and on the spaces between the veins. The epidermal cells from which they originate (Fig. 35, *D*) may be very thick-walled; they are often arched cupola-like.

Pedicularis hirsuta L.

Alcohol-material from numerous localities both in East and West Greenland, collected by E. Warming (11. 7. 1884), C. Ryder (11. 7. 1886 and 5. 7. 1887), S. Hansen (2. 7. 1888), N. Hartz (1. 9. 1891) and A. Lundager (29. 6. 1907, 17. 6. and 20. 6. 1908); also from Spitzbergen (Belsund, leg. Nathorst, 1. 7. 1888) and Norway (Talvik near Alten, leg. E. Warming, 17. 7. 1885).

Herbarium-material from Greenland, Ellesmere Land, Grant's Land, Spitzbergen, Nova Zembla and Northern Norway (Alten).

Lit.: Lange, 1871, pp. 253 et seq, 266, tab. III, fig. 21 (the seed); 1880, p. 76; 1887, p. 262; Nathorst, 1883, p. 10; Warming, 1886, pp. VII, VIII, 21, 44 and 54; 1888, pp. 35, 39, 59, 71, 74, 87, 97 and 103; 1890, pp. 206, 208 and 213; Rosenvinge, 1892, p. 686; 1896 (II), p. 78; Hartz, 1894, pp. 32 and 34; 1895 (I), pp. 116, 128, 167, 170, 171, 175, 225, 247 and 288; 1895 (II), pp. 335, 359 and 372; Hartz and Kruuse, 1911, pp. 339, 342, 343, 345, 347, 348, 353, 359, 364, 370, 375, 376, 378, 385, 402, 405, 409, 416, 418, 419, 423 and 428; Norman, 1895, p. 458; Ekstam, 1897, pp. 118, 168 and 180; 1899, pp. 7, 33, 37, 40, 48 and 50; Kruuse, 1898, pp. 350, 373, 380, 386, 394 and 398; 1905, p. 176; 1906, p. 249; 1911, in part IV pp. 196, 202, 244, 254, 266, 269 and 272, besides notes in the preceding parts;

Abromeit, 1899, p. 43; Knuth, 1899, p. 190; Andersson and Hesselman, 1901, p. 16; Cleve, 1901, pp. 10, 39, 57, 69, 70, 72, 76, 82, 83 and 88; Dusén, 1901, p. 39; Eastwood, 1902, p. 290; Porsild, 1902, pp. 110, 114, 124 and 216; 1910, pp. 259, 267 and 271; 1912, pp. 382 and 385; 1920, p. 143; Sylvén, 1905, p. 88; Simmons, 1906, p. 27, tab. II, figs. 7—8, tab. III, fig. 1; 1913, pp. 123, 137 and 164; Ostenfeld and Lundager, 1910, p. 31; Ostenfeld, 1915, p. 381; Lundager, 1917, pp. 360, 394, 399 and 402; Resvoll, 1917, p. 214.

Spot-bound, sympodial hemicryptophyte of semi-rosette type, with primary root of long duration, attaining as much as 2 cm in thickness and often furnished with some vigorous branches. As recorded by Th. Resvoll, in older specimens adventitious roots can be developed.

Sylvén describes only mere seedlings. The seed germinates in spring; during the summer a rosette consisting of a few small foliage-leaves, is formed, and the young plant enters upon its winter-rest with its shoot-apex protected by 4—6 bud-scales (Th. Resvoll): the following summer a rosette of more abundant leaves is formed, then again bud-scales and so on, until the time of flowering is reached. A flower-bearing shoot-portion with elongated internodes terminates the growth of the main axis. Also as Th. Resvoll remarks, during the flowering year, no rosette of radical leaves is formed. As regards the length of the first vegetative stage, the said author has found, that two-year-old plants had not yet any floral organs developed in the terminal bud.

At the rhizome-portion of the floral shoots, 1—3 innovation-shoots are developed — most frequently two; the succession of shoots with short internodes which are thereby formed, gradually brings about the formation of a "rhizoma multiceps" (a mesocorme).

The innovation-shoots pass through a vegetative-stage of two years duration before flowering; every summer, a rosette consisting of a few foliage-leaves, is formed and, as

in the main shoot, bud-scales, for the protection of the winter-buds. In the adventitious shoots, also, no rosette of fresh foliage-leaves occurs in the flowering year.

I have been so fortunate as to have Arctic material at my disposal, collected as late as on the 1st of September (Danmarks Ø, leg. Hartz); it contained both buds which would flower next year, and also younger buds. The former were of a considerable size (1.5 cm long, 1 cm thick); ex-

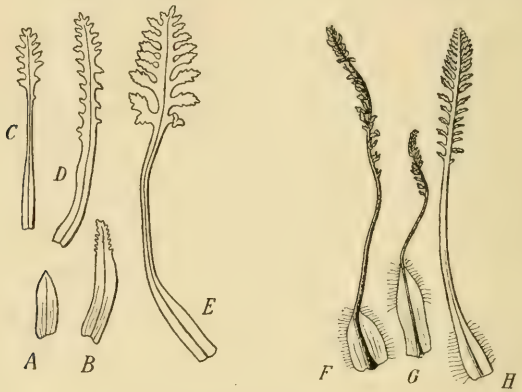

Fig. 36. *A—E, Pedicularis hirsuta.*
A, A bud-scale. *B*, Transitional form between bud-scale and foliage-leaf. *C* and *D*, Leaves from a part of the stem with elongated internodes. *E*, Rosette-leaf. (Greenland).
F—H, Pedicularis lanata.
F, A lower and *G* an upper leaf from the rosette of the same year. *H*, A leaf from the part of the stem with elongated internodes. (Greenland). All about nat. size.

ternally they were protected by the somewhat broadened bases of the dead leaves of the rosette, then followed 10—12 arched, pointed bud-scales, 10—13 mm long, and 5 mm broad, and hairy along their edges; the outermost of these bud-scales were withered. The young foliar organs were already large, and in the axils of the subtending-leaves of the inflorescence were floral buds about 0.5 mm in size, all enveloped

in non-glandular hairs. The purely vegetative buds were in all cases smaller, and the bud-scales fewer in number; also in them the young foliar organs were well-developed.

In Fig. 36 are shown 2 bud-scales (of which the one, *B*, was uppermost in a bud, and shows a rudimentary leaf-blade), a rosette-leaf and 2 leaves from the part of the shoot with elongated internodes (both kinds of foliage-leaves vary greatly in form). The leaves are hairy, especially at the base, and the stems also are abundantly covered with hairs, especially in the upper part.

The height of the flowering plant may vary greatly. From Spitzbergen (leg. Th. Wulff) I had specimens scarcely 2 cm high, which nevertheless bore as many as 4 flowers of normal size. It appears that during the end of the flowering period, a rather considerable elongation of the stem, especially of the upper part, takes place; two fruit-bearing specimens from Greenland (Amitasiarsak Fjord) were as much as 36 cm high.

The development of a "rhizoma multiceps" causes a somewhat tufted growth of the species. One specimen from Hvalrosodde (North-east Greenland, leg. Andr. Lundager) had at the same time as many as eleven flowering shoots, numerous leaf-rosettes and ten dead inflorescence-axes from previous years. This tuft-forming growth must afford additional protection to the winter-buds, the latter being covered by the numerous withered leaves.

Haustoria are found on the roots; according to Rosenvinge this species is parasitic on *Vaccinium uliginosum* and *Salix herbacea*, for example.

In the fresh condition the root has a slightly yellowish colour, and a somewhat sweetish taste (Nathorst). The radiating clefts, which are formed in the tissue of the root,

especially in the cortex (see below), are, during the winter, found to be full of ice (M. Porsild, *in litt.*).

The structure of the flower will be evident from Fig. 37 (= Warming, 1886, fig. 12). *A* shows a flower seen from

Fig. 37. *Pedicularis hirsuta.*
A and *B* (the same flower) as well as *C*—*F* and *K*—*N* are drawn from Greenland material; *I* from a flower from Northern Norway (leg. Nyhuus), *O* and *P* from flowers from Spitzbergen (leg. Nathorst). (Cf. text.) (E. Warming, 1886.)

the side; *B* the same flower, and *K* another flower, both in front view: in *A* the densely hairy calyx should be noted, the short corolla-tube, the short, warty revolute portion of the edge of the upper lip and the ridge which passes downwards from its uppermost point, into the back of the corolla-tube; also the two convexities on the lower lip, and the

furrow between them; in *B* the slightly oblique lower lip should be noted and the wide slit (as much as 2 mm) between the two revolute portions of the edge of the upper lip: here the stigma protrudes just beyond the tip of the helmet. *C* shows the curving of the upper part of the style, in *E* is seen its natural and usual position in relation to the helmet and anthers. A flower of somewhat different structure is shown in *I*: there the style is shorter, less curved, and does not reach down underneath the anthers. *D* and *F* are opened anthers, *G* stigmatic papillæ and *H* germinating pollen-grains. Honey is secreted by the three-lobed swelling on the front of the oblique ovary (*P*).

Peloria may occur: such a flower is shown in *N*; there the corolla is irregularly 6-lobed, the stamens are of equal length, and the style protrudes far, and is erect.

In very small-flowered specimens brought by Nathorst from Spitzbergen, E. Warming found as close contact of stigma and anthers, as shown in *O*.

"The corolla is of a pale rose-colour, with darker throat and tip of helmet, more seldom the colour is pure white (for instance in Upernivik). The flower is set almost horizontally. The corolla-tube is . . . . 7—8 mm long; the total length of the flower is about 13—14 mm. Slight protogyny appears to occur, and the stigma probably protrudes somewhat more in the younger flowers than later on, so that cross-pollination may perhaps take place in these" (E. Warming, 1890, p. 213). According to information given by M. Porsild it is common in Northern Greenland for the corolla to be of a whitish shade or, at any rate, of a pale pink colour. Ekstam records this species from Nova Zembla as scentless, but from Spitzbergen, as having a strong perfume. Like all the species of *Pedicularis* mentioned here, it must be assumed originally to have been adapted to pollination by humble-

bees, but insect-visitors are rare in Greenland (M. Porsild, *in litt.*), nor are they common in Northern Norway (Ekstam, 1897, p. 175); from Spitzbergen humble-bees are absent (Aurivillius). In spite of this, the species regularly sets fruit everywhere; it must also be said to be *the* one of the Arctic *Pedicularis spp.*, which is best fitted for self-pollination.

In flowers like *E* and *O* (less, it is true, in *I*) self-pollination is inevitable.

The seeds are described and figured in Lange, 1871 (tab. III, fig. 21).

Geographical Distribution: West Greenland from 64° and northwards, rare between 64° and 68°; East Greenland from 65° and northwards (rare in the district of Angmagsalik); Arctic North America (the continent and the islands), Arctic Siberia and Russia, Nova Zembla and Spitzbergen, the mountain summits of northern Scandinavia.

In Greenland, according to the numerous records in the literature, it appears that the species makes no great demands as regards the nature of its habitat. Thus it can be found on heaths, mossy flats, herb-slopes, in coppices and in fissures in fields where the surface is cracked into polygonal cakes (rudemark) (Lange, Warming, Hartz, Kruuse and M. Porsild), according to the last author also in gravelly barrens (1920, p. 143). In Greenland this species can dispense with a snow-covering during winter, and it is there a decided sun-plant, (M. Porsild), and has not its proper home in the snow-troughs.

According to Norman, in Northern Norway it prefers gravelly, not grass-covered localities, and there it has not hitherto been found where the aspect is sunny, but only on the northern and indifferent (eastern and western) sides of the mountains; it belongs there to the flora of the snow-troughs (Th. Resvoll). A. Cleve also remarks: "Bedarf sehr wenig Insolation

und meidet sogar die sonnig trockene Wiese"; the species is otherwise characterized as "häufig in der Heide, insbesondere die frischere Andromeda-H., gern in schattigen, schneereichen Mulden, vom Plateau das Gebirge emporsteigend, Ferner in der Sumpfwiese und auf den Moorhümpelen, aber einerseits ins Moor nicht hinabsteigend, anderseits nicht auf trockener, vegetationsarmer Felsenflur. Ein verfilzter Humusboden ist unbedingt notvendig." In Greenland this species is a decidedly spring-flowering plant, but, as an exception, flowering specimens may be found throughout the summer according to the point of time at which the snow melts at the place in question. Hartz found it on Danmarks Ø with the flowers still in bud on the 1st of September, and expressly remarks that it was "on quite recently-bared ground, at the foot of the snow-drift."

Anatomy. The Root. Fig. 38, *A* and *B*, shows portions of the transverse section of a root, about 4 mm thick. The epidermis decays very quickly — as described by Hovelacque for the root of *Pedicularis palustris* — the epidermal cells have already collapsed in roots not more than one mm in thickness, and in the root figured they have disappeared completely. The uppermost layer in Fig. 38, *A*, is the outermost layer of the primary cortex, which, on the whole, only consists of 4—5 cell-layers. The cells have been very greatly elongated tangentially during the secondary growth in thickness, and are divided by a great number of thin radial walls; the primary cortex persists for a long time, I found it even on roots about one cm thick. The outer walls of the outermost layer are cuticularised. At the stage of development figured in Fig. 38, an endodermis is not recognizable; in quite young roots faint Casparian dots can be demonstrated. The structure of the secondary cortex is very characteristic, since there is found in it a circle of radiating clefts, of which two

are seen in *B* (26 such clefts — most of them larger — occurred in the root figured) by which all the phloëm-tissue of secondary formation is split into a corresponding number of radii, which in their outermost parts appear to be somewhat crumpled together, evidently by pressure of the tissue later on formed by the cambium. In these radii the groups of sieve-tubes are flanked on both sides by parenchyma. Within the cambium some groups of vessels are seen; corresponding to each ray of tissue in the cortex 1 or 2 rays of groups of vessels occur in the xylem, divided reciprocally by broad radii of parenchyma, in which the clefts from the phloëm may be continued, and may reach almost to the centre of the root.

Fig. 38. *Pedicularis hirsuta.*
A, Transverse section of the outermost layers of the cortex of the root. *B*, Transverse section of a portion of the stele of the root. (Greenland.) (*A* and *B* about $^{110}/_{1}$.)

The portion of the stem with elongated internodes shows a thin-walled epidermis with stomata; the cortex is few-layered, and its cells contain chlorophyll-grains. When the

stem has reached its full development (i. e. at the end of the flowering period), there is found in the stele a continuous, but narrow ring of vessels and a few layers of wood-fibres, strengthened internally by the outermost layers of the pith,

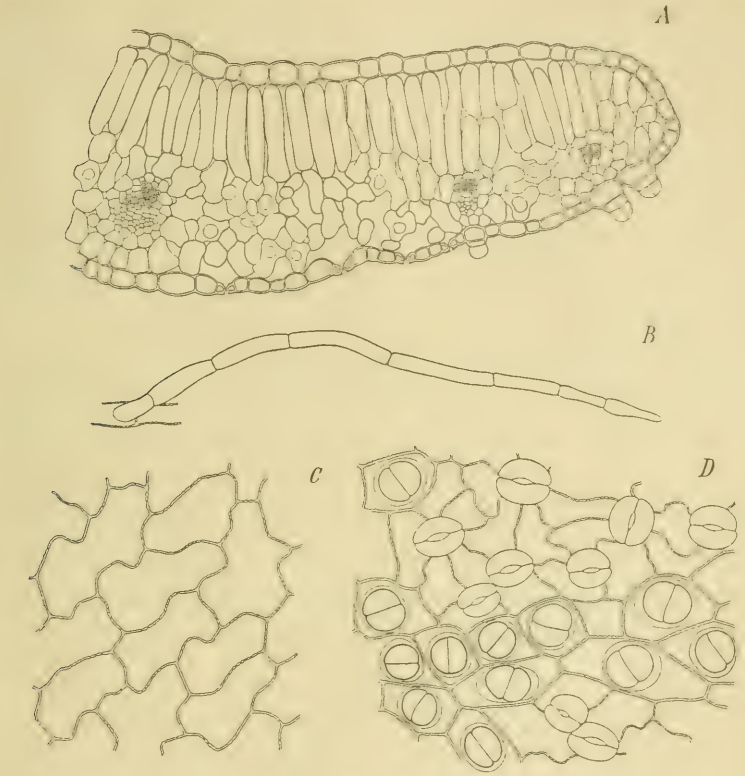

Fig. 39. *Pedicularis hirsuta.*
A, Transverse section of the leaf. *B*, A non-glandular hair from the basal portion of a leaf. *C*, Epidermis of the upper, and *D* of the lower surface of the leaf. (Greenland.) (*A* about $^{110}/_{1}$; *B* about $^{70}/_{1}$; *C* and *D* about $^{220}/_{1}$.)

the cell-walls of which become somewhat thickened and lignified; the central part of the pith dies away. In the basal part of the stem which bears the leaf-rosettes (the mesocorme), a transverse section shows a circle of vascular bundles with

intervening parenchyma-rays. Secondary growth in thickness takes place, and in connection with this a similar cleft-formation in the phloëm as in that of the root. The pith is wide, and does not die away.

The Leaf. The epidermal cells of both the upper and lower surface have thin, finely porose and almost straight to slightly wavy lateral walls (Fig. 39, *C* and *D*). Stomata occur only on the lower surface; they are surrounded by 4—6 cells. The transverse section shows 1—2 layers of well-developed palisades and a spongy tissue consisting in part of rather copiously branching cells (Fig. 39, *A*). Non-glandular hairs of the type shown in Fig. 39, *B* occur both on the stem and leaf; they are found in particularly great numbers on the basal portions of the foliage-leaves of the portion of the stem with elongated internodes, and on the leaves subtending the flowers, but more sparingly on the basal portion of the rosette-leaves proper, and only singly on the leaf-lobes, and then always on the upper surface. On the epidermis of the lower surface, under the branches of the veins of higher order, glandular hairs of the usual type are found; the epidermal cells upon which the glandular hairs are seated, have straighter, thicker and more highly porose lateral walls, than have those which surround them.

Chlorophyll was present in abundance in the whole of the mesophyll and was also found in the epidermis of the lower surface.

No difference could be observed as regards the anatomical structure of the leaves of the rosette and of those on the portion of the stem with elongated internodes.

Pedicularis lanata (Willd.) Cham. & Schlecht.

Alcohol-material from Greenland (Amerdlok, 15. 7. 1884, leg. Th. Holm; Kingartak, 25. 7. 86, leg. Ryder; Pröven, 24. 6. 1888, leg. Myhre).

Herbarium-material from Greenland, King William's Land, Ellesmere Land, Arctic North America, Nova Zembla and Arctic Siberia.

Lit.: Lange, 1880, p. 76; 1887, p. 262; Nathorst, 1883, p. 10; Warming, 1886, pp. VII, VIII, 21, 44, 47 and 54; 1888, pp. 59, 74, 87 and 104; 1890, pp. 206, 208, 210 and 213; Rosenvinge, 1892, p. 687; 1896 (I), p. 68; Hartz, 1894, p. 45; 1895 (I) p. 306; 1895 (II), p. 372; Kruuse, 1898, pp. 350, 373, 380, 394 and 398; 1906, p. 249; 1911, pp. 103, 132, 196 and 207; Abromeit, 1899, p. 44; Ekstam, 1899, pp. 7, 32, 37, 40, 48, 49 and 50; Knuth, 1899, p. 193; Andersson and Hesselman, 1901, p. 16; Eastwood, 1902, p. 291; Porsild, 1902, pp. 114, 178; 1910, pp. 259, 267 and 270; 1912, pp. 382 and 385; 1920, p. 143; Simmons, 1902, p. 29, tab. II, figs. 1—3; 1906, pp. 124, 137 and 164.

Spot-bound, sympodial hemicryptophyte of the semi-rosette type; like the foregoing closely related species, it has a thick, scantily branched main root of long duration; adventitious roots are probably, as a rule, only slightly developed. As *P. hirsuta*, this species can form large and dense tufts.

It appears that the first vegetative-stage may be confined to two years, so that the main axis of the young plant, after the formation of two consecutive leaf-rosettes, can, in the third summer, form a shoot-portion with elongated internodes, although a comparatively weak one, terminating in an inflorescence. Generally, the necessary vegetative-stage preceding the flowering is, no doubt, of longer duration. The vegetative stage of the innovation-shoots extends as a rule over 2 years.

P. hirsuta and *P. lanata* differ essentially from each other by the fact that the latter has no specially-developed

bud-scales, but protects its young buds during the winter with the broad, arched, very persistent bases of the rosette-leaves developed during the growth-period of the preceding summer, which bases are densely hairy along their edges; the rosette-leaves formed towards the end of the growth-period, are especially distinguished by their large basal-portions. Fig. 36, *G* shows such a leaf. On the other hand, the stalk and blade of the leaf illustrated in Fig. 36, *G* are essentially smaller than those in Fig. 36, *F*, which is a previously developed leaf from the same rosette; the leaf-blade may be even smaller than in *G*, but I do not think it is ever wholly wanting.

The leaves upon the uppermost portion of the shoots where the internodes become elongated, have not such broad bases (Fig. 36, *H*).

The rosettes are rich in leaves; at the base of a fairly vigorous flowering shoot I counted 60 withered leaves or remnants of such; also the above-ground portion of the stem is abundantly covered with leaves, especially below, although it cannot be said that the shoots have any true radical rosette of fresh leaves in the flowering year. The rosette-leaves, when withered, are very persistent, and may remain for several years, black and crumpled, at the base of the shoots (Fig. 36, *F* and *G* are two such withered leaves); naturally, this contributes towards making the tufts denser, and the protection of the young buds more effective.

The root is intensely yellow in colour, and has, as already stated by Nathorst, a sweetish taste, almost like that of carrots. It is used as an article of food by the Smith-Sound Eskimos[1] and by the Chuckes (Kjellman, 1882 (III), p. 366).

The structure of the flower is shown in Fig. 40, *A*—*D*

[1] P. Freuchen: Om Plantekost hos Smith-Sund Eskimoerne. Geografisk Tidsskrift. Kjöbenhavn. Bd. 24. 1917—18. p. 310.

(the drawing is executed after a sketch by Eug. Warming made from material from Greenland). In *A* and *B* the flower is seen from the side, the position of the stamens is indicated in *A*; in *B* the ridge reaches highest above the uppermost edge of the revolute portion of the margin of the upper lip; of the three lobes of the lower lip, the middle one is the smallest. The lower lip is not oblique; the two convexities are quite glabrous. *C* shows a flower in front view, the narrow furrow between the convexities should be noted. *D*, a pair of stamens; here the filaments of both stamens are hairy; this feature varies, sometimes only the two longest are hairy. In this species also there occur nectary-protuberances at the base of the ovary.

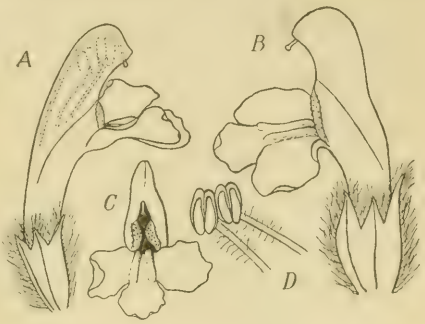

Fig. 40. *Pedicularis lanata.* *A* and *B*, Flowers seen in side view; in *A* the position of the anthers and the style is indicated; the hairs of the calyx are drawn only along the outlines of the figures. *C*, The uppermost part of a flower in front view. *D*, A pair of anthers. (Greenland.) (*A*, *B* and *C* about $^2/_1$; *D* about $^5/_2$.) (After E. Warming.)

"This species is still more conspicuous (than *P. flammea* and *hirsuta*) on account of its richly and densely flowering inflorescence, and the bright pink colour of the flowers; the tip of the upper lip and the throat are darker in colour than the rest of the flower. It has also a slight scent, and the flowers are considerably larger than those of the two foregoing species (*P. flammea* and *hirsuta*), having, namely, a total length of 2 cm, and a corolla-tube-length of 12—13 mm . . . . The flower stretches out considerably, it may even be almost horizontal. The stigma projects out of the flower,

and will evidently be easily touched by an insect visitor. the anthers are placed immediately behind the stigma and, on account of the stretched-out position of the flower, partly above it, so that self-pollination will probably take place" (E. Warming, 1890, p. 213). The same author describes a flower from Spitzbergen with pelorial development.

On Spitzbergen (forma *dasyantha*) Ekstam found the end of the style to be rolled up (as in *P. hirsuta*, cf. Fig. 37), so that the stigma is in contact with the anthers. In my material I always found it to be protruding, as also shown in the figure.

Varieties with entirely white flowers may occur, but they are very rare (M. Porsild, 1920).

The species is fragrant (Ekstam and Warming). It sets fruit everywhere abundantly and regularly, and also in Spitzbergen, where humble-bees, its natural pollinators, are wanting (Aurivillius); according to information given by M. Porsild, insect-visitors are rare in Greenland. Among the Eskimos the plant is known for the abundance of honey contained in its flowers; at Cape York its popular name is: "The food of the humble-bees;" and children pick the flowers and suck the honey out of them or even eat them entire (Freuchen, l. c.).

During the end of the flowering-period, the axis of the inflorescence elongates.

Geographical Distribution. The species is common in West Greenland, from Disco Bay and northwards. "In N. Strömfjord it is restricted to alpine stations and northern slopes and rather scarce (P & E). South of Holsteinsborg observed several times down to Itivdlinguaq, 66°30′ (P & E)" (Porsild, 1920); from East Greenland it is totally absent (Porsild, l. c.). It is also found in Arctic North America (the continent and the islands), the western Subarctic North

America, (the Rocky mountains), Arctic Asia, Nova Zembla and Spitzbergen. The species prefers fairly dry habitats. M. Porsild records that it is found "on rocky flats and on heaths" (1912, p. 382). "In poor and open heath, often in gravelly barrens far away from other plants. When growing

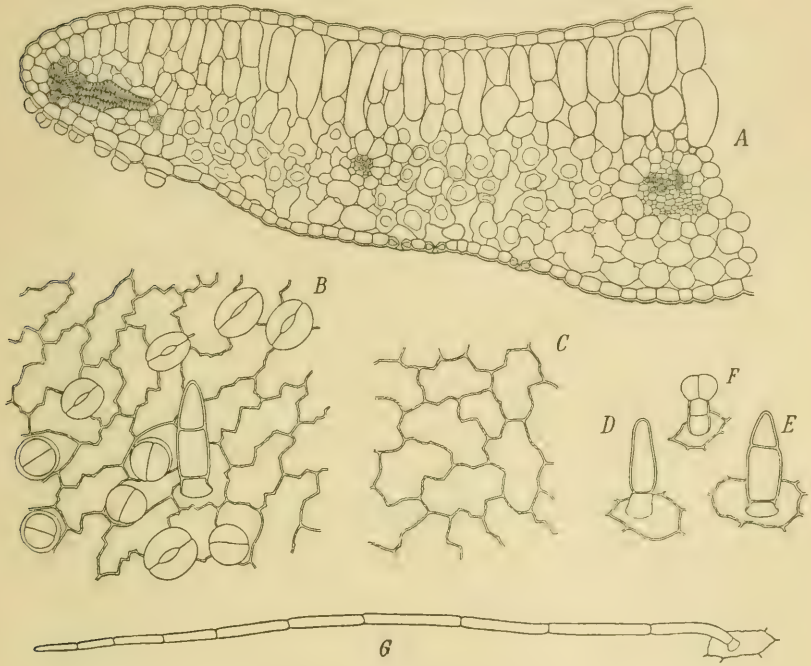

Fig. 41. *Pedicularis lanata.*
A, Transverse section of the leaf. *B*, Epidermis of the lower, and *C* of the upper surface of the leaf. *D* and *E*, Non-glandular hairs from the lower surface of the leaf. *F*, A glandular hair from the stem. *G*, A non-glandular hair from the basal portion of leaf. (Greenland.) (*A* about $^{110}/_{1}$; *B*, *C*, *D*, *E* and *F* about $^{220}/_{1}$; *G* about $^{70}/_{1}$.)

amongst other plants, however, the roots also of this species are provided with *haustoria*" (1920, p. 143). During the winter, although the plants in themselves are often bare of snow (l. c.), yet the dense tufts always catch some snow between the numerous decaying leaves, and this naturally

affords some protection to the winter-buds (M. Porsild *in litt.*). According to the same author, in the same locality, the species flowers 1—2 weeks before *P. hirsuta* (1920, p. 143). On Spitzbergen, according to Ekstam, it is found "auf trockenen, starker Insolation ausgesetzten Abhängen."

In anatomical respects, the root and stem agree closely with the corresponding organs in *P. hirsuta*. The anatomy of the leaf is shown in Fig. 41, *A*—*G*. In the transverse section 1—2 layers of short and broad palisade-cells are seen, and a spongy parenchyma, which consists of distinctly branched cells. *B* shows a portion of the epidermis of the lower surface, and *C* a similar portion from the upper surface of the leaf. The lateral walls are thin and finely porose; stomata are found only on the lower surface of the leaf and the guard-cells occur on a level with the leaf-surface. On the basal portion of the leaf, the cuticle is thicker than on the stalk and the lobes, and it is furnished with fine striations. Chlorophyll occur in abundance in the mesophyll, and also in the epidermis of the lower surface.

The glandular hairs in this species are almost exclusively confined to the edges of the leaf-sections; in *A* is seen exteriorly to the left, a group of the tracheidal tissue in which the branches of the veins end, and in connection with which the glandular hairs occur. The structure of these is similar to that in the other species; the epidermal cell from which the glandular hair is developed, has not, however, in *P. lanata*, much thicker or more highly porose walls, than have the epidermal cells, which surround it. Non-glandular hairs of the type shown in *G* occur in abundance on the edges of the leaf-bases, on the stem and, in the floral region, on the scale-leaves and calyx, more scantily on the leaf-stalk, and on the upper surface of the leaf-blade. On the lower side of the leaf-lobes there are small non-glandular

hairs (Fig. 41, *B*, *D* and *E*) intermingled with the glandular hairs; on the petiole and stem are glandular hairs of the form shown in Fig. 41, *F*.

Pedicularis flammea L.

Alcohol-material from Greenland (Godthaab, leg. E. Warming, 29. 6. 1884; Christianshaab, leg. S. Hansen, 2. 7. 1888; Proven, leg. Myhre, 2. 7. 1888; Danmarks Ø, leg. N. Hartz, 18. 2. 1892), Iceland (Hvitarvattn, leg. A. Feddersen, 3. 6. 1886), and Northern Norway (leg. Nyhuus, 1885).

Herbarium-material from numerous places in East and West Greenland, from Norway, Iceland and Arctic America.

Lit.: Lange, 1870, pp. 254 et seq., 266, tab. III, fig. 22 (the seed); 1880, p. 75; 1887, p. 262; Warming, 1886, pp. VII, VIII, 44, 47 and 54; 1888, pp. 27, 34, 39, 59, 87, 90, 104, 130 and 133; 1890, pp. 207, 208 and 211; Rosenvinge, 1892, p. 686, 1896 (II), p. 128; Hartz, 1894, pp. 11, 32 and 43; 1895 (I), pp. 165, 170, 171, 175, 188, 247, 256, 288 and 290; 1895 (II), pp. 335, 359 and 372; Hartz and Kruuse, 1911, pp. 338, 342, 347, 357, 359, 378, 379, 380, 385, 409, 411, 423 and 428; Børgesen, 1895, pp. 223 and 225; Norman, 1895, p. 458; Kruuse, 1898, pp. 350, 373, 379, 394 and 398; 1905, p. 176; 1906, p. 248; 1911, in part IV pp. 196, 243, 254, 255 and 274 besides notes in the preceding parts; Abromeit, 1899, p. 43; Knuth, 1899, p. 190; Cleve, 1901, pp. 18, 39, 57, 72, 76 and 88; Dusén, 1901, p. 39; Porsild, 1902, pp. 114, 175, 178, 187, 216; 1910, p. 267; 1912, pp. 382 and 387; 1920, p. 142; Ostenfeld and Lundager, 1910, p. 31; Simmons, 1913, pp. 124 and 140.

Spot-bound, sympodial semi-rosette hemicryptophyte, with short, vertical mesocorme which dies away behind, and a rather abundant development of adventitious roots.

The first vegetative-stage fairly commonly appears to extend over 4 years — in the case of one individual (Disco) I found it to extend over 3 years, and in the case of another (Iceland) 6 years. A short, vertical mesocorme is developed during the first vegetative stage; the main root is still present during the first flowering-period, but dies away afterwards.

The winter-buds are provided with a number of bud-scales; these as well as the foliage-leaves leave real leaf-scars on the mesocorme on decaying. Adventitious roots are developed rather abundantly, especially from the basal part of the mesocorme, they generally occur in connection with innovation buds; the adventitious roots are somewhat swollen.

The innovation-buds arise from the axils of the scale-leaves; the lower buds on the mesocorme do not generally develop any further, but remain as reserve-buds; as in *P. Oederi* it is the buds which occur in the axils of the innermost scale-leaves formed during the summer previous to that in which the parent-shoot flowered, which are the most vigorously developed. Usually only two of these buds expand, but the number may be more, in a single case I counted as many as 6.

During their first summer the adventitious-shoots always bear two fully-expanded foliage-leaves; as in the main-shoot the terminal bud is protected by scale-leaves. In case flowering does not take place in the following year, — it may occur, but no doubt only exceptionally, — a rosette of foliage-leaves is developed, followed in turn by scale-leaves, and then, after passing through still another winter the shoot, in the majority of cases, succeeds in flowering.

In a specimen from Ignerit (Greenland) in which 2 of the basal buds on the mesocorme had developed further, one of them had formed rosettes of foliage-leaves for 4 successive summers, and the other for even 5.

In a winter-bud (the specimen in question was collected by N. Hartz, on the 18th of February 1892, on Danmarks Ø, East Greenland) there were found young foliar organs and flowers, all of which were highly developed; in the young flowers the separate parts were quite distinguishable

under the microscope. The shoot which was terminated by this winter-bud, was one year old — consequently, the length of the purely vegetative period in this case will only have been one year — during the previous year it had, as is usually the case, unfolded 2 foliage-leaves; the bud-scales numbered 5.

The maximum height of the flower-bearing shoot was found to be 28 cm; from Iceland and Greenland I found small individuals, flowering for the first time, which were only 3 cm high. A specimen from Disco differed entirely by a total absence of foliage-leaves on the above-ground stem, which was 20 cm high, and by having flowers, the lowermost of which were long-stalked almost down to the base; the axis was comparatively very thick (about 8 mm in diameter).

E. Warming found the flowers from Norway (W. Finmark), Iceland and Greenland to agree entirely in structure; from his descriptions I quote the following: "The flowers are not very conspicuous; their lower part stands erect, almost parallel with the axis of the inflorescence, their upper part is bent slightly forward (Fig. 42, *A*); the colour is yellow, the upper part of the helmet is, however, more or less reddish-brown. The corolla-tube is only 7—8 mm long; the lower lip is very small, with three rounded lobes, and often appears smaller still by the fact of its edges being bent backwards (Fig. 42, *C*). The cleft of the upper lip is sometimes very narrow ($^1/_2$ mm, see Fig. 42, *D*), but sometimes wider, even so wide that there is a large entrance to the interior of the flower, as for example in flowers with an upper lip curved strongly forward.

This species appears to be as highly adapted to self-pollination, as it is poorly adapted to insect-pollination, which also agrees with the fact that it is so little conspicuous. I never saw the stigma protrude from the blunt, untoothed tip; so it is placed immediately in front of, or slightly under

the anthers (Fig. 42, *F*). The fact that in many flowers I have found the stigma covered with pollen-grains, some of which were germinating, and have found abundance of pollen around the anthers, even in a flower like *A*—*B*, in which the stigma is situated so unusually high above the anthers, is a justification for regarding this as brought about by self-pollination. I must, however, point out the fact that the

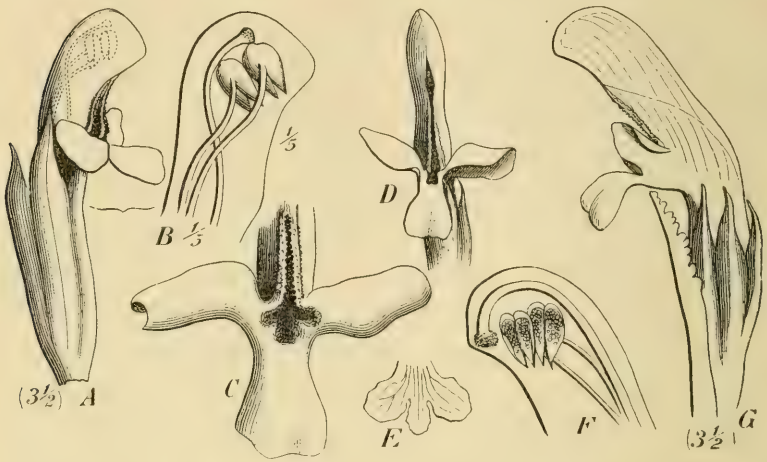

Fig. 42. *Pedicularis flammea.* (Greenland).
A, A flower in natural position in the inflorescence; *B* (⁵/₁), the upper part of the same in longitudinal section. *C*, Lower lip and the part around the throat seen in front view. *D*, The upper part of a flower in front view. *E*, Lower lip, slightly magnified. *F* as *B*, but with the stigma in another position. *G*, A flower in natural position, larger than *A*, showing the venation of the upper lip. (E. Warming, 1890.)

stigma is not placed in the same position relative to the anthers in all the flowers of the same inflorescence, and it appeared to me to be the rule for it to be situated slightly more forward in younger than in older flowers; . . . . the filaments are glabrous. In many places in West Greenland, as far as Upernivik (Ryder), it was found with abundant fruit. Even in July (1884) new fruit was set at 64° and 67° N. lat."

I can add to the above that in older flowers the helmet often appears to bend forward, as described by Kerner in the case of *P. Oederi*.

In the material at my disposal, both from West and East Greenland, there were many fruiting specimens. That it really is the rule for the stigma to be enclosed in the helmet, is seen among other things, by the fact that Blytt in his "Haandbog i Norges Flora" gives this as a specific character.

Geographical Distribution: West and East Greenland (rare in South-west Greenland according to Rosenvinge, in East Greenland even as far north as Germania Land according to Ostenfeld and Lundager), Iceland, Arctic and Subarctic North America, Arctic Russia and the mountainous regions of Northern Scandinavia.

As regards the habitat of *P. flammea*, many notes are to be found scattered in the literature on the subject. A. Cleve states that in the district of Northern Sweden investigated by her, it was found "nur auf den Moorhügeln und in Sumpwiesen zusammen mit der vorigen (*P. hirsuta*), welche diese Art nicht bis in die trockene Heide zu begleiten vermag, ebensowenig wird sie auf dem N. Abhang oder in der Nähe von spät schmelzendem Schnee gefunden." In Northern Norway it is found, according to Norman, only on the northern and on the indifferent (eastern and western) sides of the mountains. In West Greenland it grows, according to E. Warming, in willow-coppices where it may be said to have its home, and also on herb-flats, on heaths (parasitically on *Vaccinum uliginosum* and *Salix herbacea*) and in grassy bogs. Porsild has also found it on slightly damp moss-heaths. N. Hartz and Kruuse record it from East Greenland as growing on herb-slopes and rocky flats, in carpets of prostrate *Betula nana* and *Vaccinium uliginosum*, on knolls in bogs, and on damp heaths. According to Hartz

(1895 (II), p. 335), its habitat is snow-covered during winter; the plant is mentioned as common in the interior of the fjords, but absent further eastwards, out towards the open sea. Dusén records practically the same, and he also knows it only from a single habitat in the coast-land outside the fjords (Cape Borlase Warren). A. Cleve considers it to belong to the "Gruppe der späteren Frühlingspflanzen." In Greenland it is a middle-summer-flowering plant (M. Porsild).

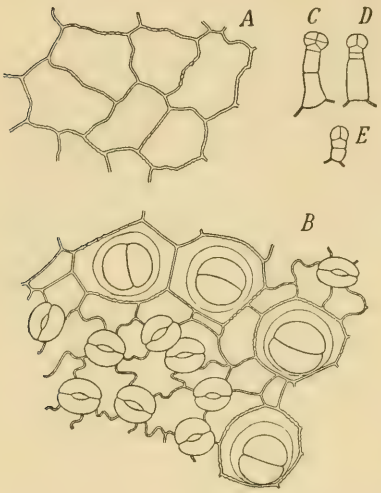

Fig. 43. *Pedicularis flammea.* *A*, Epidermis of the upper surface of the leaf; *B*, of the lower surface of the leaf. *C*, *D* and *E*, Glandular hairs; *C* and *D* from the upper surface and *E* from the lower surface of the leaf. (Greenland.) (*A* and *B* about $^{220}/_{1}$; *C*, *D* and *E* about $^{70}/_{1}$.)

The Anatomy of the root and stem agrees exactly with that of the corresponding organs in *P. Oederi*. The parenchyma of the root contained a great abundance of amylodextrin-starch.

The surface-view of upper and lower epidermis of the leaf is shown in Fig. 43, *A* and *B*; the pores of the lateral walls were always found to be rather faint. The transverse section of the leaf agrees exactly with that of *P. Oederi*. Non-glandular hairs are absent; in addition to the glandular hairs of the usual *Pedicularis*-type, such forms are also found as are shown in Fig. 43, *C*, *D* and *E*; *C* and *D* occur scattered, especially on the upper surface of the leaf, and *E* on the lower surface of the segments, especially along their main vein and lateral veins

of 1st order. Chlorophyll-grains occur abundantly in the whole of the mesophyll, and also in the epidermis of the lower surface.

Pedicularis Oederi Vahl.

Alcohol-material from Norway (Kongsvold (Dovre), leg. E. Warming, 13. 7. 1887; Muggrubfjældet near Roraas, leg. Thekla Resvoll, 29. 7. 1918).

Herbarium-material from Nova Zembla, Arctic Siberia (Khabarowa and from near the Taimyr river) and St. Lawrence Island.

Lit.: Axell, 1869, p. 102; Kjellman, 1882 (I), p. 257; 1882 (II), p. 325; 1882 (IV), p. 510; Kjellman and Lundström, 1882, p. 304; Aurivillius, 1883, p. 451; Warming, 1886, p. 47; 1890, pp. 207, 208, 210 and 214; Lindman, 1887, pp. 82 and 99, tab. IV. fig. 46; Kerner, Bd. II, 1898, p. 337; Knuth, 1899, p. 186; Sylvén, 1906, p. 89; Schröter, 1908, pp. 454, 455 and 458; Resvoll, 1917, p. 210.

Spot-bound, sympodial semi-rosette hemicryptophyte with a short, vertical mesocorme which dies away behind. Adventitious roots are rather abundantly developed.

According to Sylvén the seed germinates in spring. "The elongated hypocotyl unites with the main root, scantily branched throughout, into a peg-shaped food-storing organ which becomes rather thick at an early period. In more advanced young-plants adventitious roots, thickened by the storage of reserve food-material, like the main root, sometimes appear to be developed from the hypocotyl, or from the base of the epicotyl." Th. Resvoll has studied the whole development from seed to flowering plant: During the first summer two small foliage-leaves expanded, the terminal bud was protected by a few scale-leaves, and contained the rudiments of the foliage-leaves of the following summer; the plant passed the winter in this stage. The foliage-leaves fell off late in autumn, and left leaf-scars. "After having passed

through the winter, the young leaf-organs developed into a rosette of foliage-leaves, few in number, . . . even early in the summer the development of foliage-leaves stopped, instead of which the apex of the stem developed a terminal bud covered with scales. In this manner the plant continues through several years. The leaves, which are exceedingly small in the first summer, having blades only about 1 cm long, become larger every summer, and the number of the leaves also increases with the age of the leaf-rosette. The last summer before the plant flowers I have seen 4—8 foliage-leaves."

The shortest first-vegetative-stage observed by the author in question, extended over 3 summers, in other individuals it proved to have extended over as many as 6 summers; in one individual (from Nova Zembla) I found 3 vegetative years, another showed 7. As the leaves fall off, leaving a regular leaf-scar (as already described by E. Warming (1890, pp. 207 and 209) both for this species and for *Pedicularis palustris*) and the broader and more distantly-placed scars of the foliage-leaves can be easily distinguished from the narrower and more closely-placed scars of the scale-leaves, the individual year-growths of the mesocorme become very marked and easily observable (Th. Resvoll).

"It is characteristic of this plant, that the development takes place, so to speak, suddenly, as long as the plant is in the rosette-stage. Thus all the leaves come out almost at once, and not one by one during the summer; and as soon as the rosette has unfolded, the bud for the next summer is already seen in the middle of it. The same is also the case as regards the rosette-stage of the lateral shoots." (Th. Resvoll).

Even in the bud, the rudiments of the organs which are to expand during the next summer, attain a high degree of development. In an individual which Th. Resvoll in-

vestigated on Knutsho (Dovre) on July 23rd, the terminal bud proved to contain "the young stem for the coming summer, covered by the rudiments of the stem-leaves; within these were the subtending leaves of the flowers; the separate parts of these were already distinctly discernable."

The flower-bearing stem-portion has, as a rule, no foliage-leaves at its base, but such may occur as an exception.

In the interval between germination and flowering the plant develops a vertical mesocorme, as much as 1 cm long and 0.5 cm thick, from the lower part of which there proceed a varying number of adventitious roots (I counted as many as 8); as in *P. flammea* they are somewhat swollen, as a rule especially in their proximal half, but sometimes also along their entire length, but narrowing abruptly towards the base; they become as much as 10 cm long, and as much as 6 mm in diameter; most frequently they are furnished with slender, filiform branches, or, at any rate, scars left by such are present; more rarely with 1—2 vigorous root-branches. The main root dies away; in the majority of cases it probably does not survive the first flowering period of the individual. As mentioned by Warming (1890, p. 207), the majority of the adventitious roots arise at the base of a bud on the mesocorme. According to the observations of Warming and Th. Resvoll — which observations I am able to confirm fully — the lateral buds are developed especially in the axils of the scale-leaves, and are of the same age as these. The buds in the lower part of the stem develop two small foliage-leaves during their first summer, but usually do not develop any further; as a rule they are found as small formations covered with a few scale-leaves; they must be regarded as reserve-buds, for, as seen in a specimen from Nova Zembla, under certain circumstances they may develop further and even produce flowers.

The most fully developed buds are always found (Th. Resvoll) in the axils of the uppermost set of scale-leaves, which are found to the number of 5—10 at the base of the flower-bearing stem-portion. It is commonly the innermost scale-leaves which subtend the innovation buds, and usually only two such are found, more rarely several (as many as 7, Th. Resvoll). During their first summer they develop 2—3 rather large foliage-leaves, often followed by 1—2 quite small ones, and lastly bud-scales for the protection of the winter-bud. The buds open almost at the same time as the flowers of the main shoot.

According to Th. Resvoll, the duration of the vegetative-stage of the lateral shoots may be restricted to one year only; it is, however, longer, as a rule; for instance, on Knutshö (Dovre) the said author found 4-year-old lateral shoots, which had not as yet young floral organs in the terminal bud. In several cases also I found a vegetative stage of only one year's duration (among others in a specimen from Nova Zembla), more frequently, however, 2 or 3 years.

As the parent-rhizome dies away behind, and the lateral shoots develop adventitious roots, there is a possibility of vegetative propagation, although, of course, the plant cannot spread much by this means.

Schröter records this species from the Alps as occurring parasitically especially on *Carex firma*.

The structure and biology of the flower was first described by Lindman; since that E. Warming and Kerner have dealt with this species. Some unpublished drawings of the flower have been kindly placed at my disposal by E. Warming; the illustrations in Fig. 44, with the exception of *G* and *H*, have been made after them. *A* is characterized by its long corolla-tube, its densely-hairy calyx, (the hairs have been indicated only along the edge of the calyx),

and by its but slightly protruding stigma; in *B* the main features of the venation of the helmet are seen, to which a system of raised ridges on the outer side of the helmet corresponds. The dots on the side of the helmet in Fig. 44, *B* indicate small glandular hairs, which are especially numerous in the front part of the helmet. Fig. 44, *H* shows such glandular hair in lateral view, highly magnified; the head is 4-celled. *D* is the lower lip in surface view; the two con-

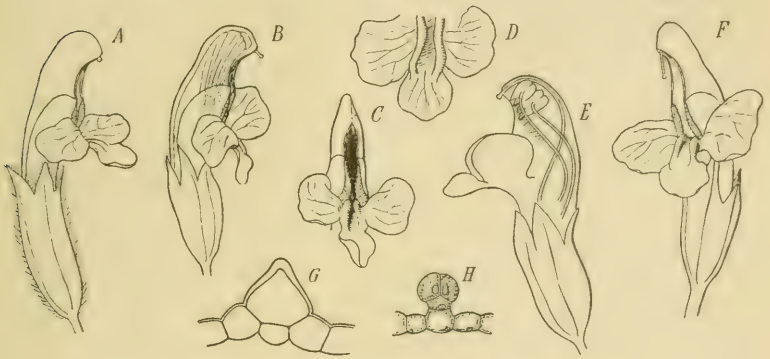

Fig. 44. *Pedicularis Oederi.*
A, *B*, *C*, *D* and *E* are drawn from flowers from Sweden; *F* is a flower from Kongsvold (Dovre). *G*, Transverse section of one of the warts from the revolute portion of the edge of the upper lip. *H*, A glandular hair from the helmet. (*A*, *B*, *C*, *D*, *E* and *F* slightly under $^{2}/_{1}$; *G* and *H* about $^{110}/_{1}$.) (Drawn by E. Warming.)

vexities are distinctly visible here, as also in Fig. 44, *C* and *F*. Fig. 44, *F* shows a flower with a very far-protruding style; in *E* the position of the stamens is seen, the filaments of the foremost pair of stamens are hairy along their upper part. One of the warts from the revolute portion of the upper lip is seen under high magnifying power in Fig. 44, *G*; on its outer surface it has strong cuticular striations, as have also the cells which surround it. The calyx, subtending leaf and axis of the inflorescence vary from glabrous to

hairy, even in individuals from the same locality (Muggrubfjældet near Röraas); the hairs are multicellular, pointed and glabrous.

I quote the following from Lindman's exhaustive description:— "The flower is 20 mm long, yellow or whitish-yellow in colour; the tip of the upper lip is dark-red on its inner side, and this colour more or less penetrates through and gives the corresponding spot on the outer side a greyish-red tint; the upper lip has often in addition on the outer side a dark-red spot on each side. The flower is quite erect and adpressed to the peduncle. . . . . The stamens agree with those in the other species; their pollen is consequently dry and loose, is fully developed even in the flower-bud, and is contained in a receptacle formed by the four convergently dehiscing anthers, which are held together by the laterally highly compressed upper lip. . . . . As in the other species the pollen is shed when an insect penetrates into the flower, and thereby widens the slit of the upper lip, which is rather narrow in this species. . . . . The nectary is in the same place as in the other species; the corolla-tube is 10—13 mm high." The position of the stigma in the flowers figured by Lindman is very much like that in Fig. 44, *B* and *F*, given here; in addition Lindman mentions flowers in which the style was so short, that the stigma remained quite inside the helmet, and did not even reach the anthers; the stigma was normally developed, however, in these flowers.

According to Kerner (p. 337) the whole of the upper lip curves forward so strongly at the end of the flowering period, that it looks as if it were broken; even if it originally stood as a continuation of the lower part of the corolla-tube enclosed in the calyx, it stands then at an angle of 70°, or even 90° with this, and by bending forward it drags down with it the style and the stamens, so that the stigma no

longer stands in front of, but below the anthers; these are no longer united, and shed their pollen spontaneously, which is scattered down upon the stigma, and effects self-pollination in case cross-pollination should fail. Lindman and Warming mention nothing regarding this point; I observed it in many inflorescences but must, however, add that the curvature may also take place in the uppermost part of the corolla-tube.

Kerner (Die Schutzmittel der Blüthen gegen unberufene Gäste, 1876) and after him H. Müller, describes the pollination of *P. recutita*, a species very similar to the present one, and, in so doing, states that the insect (humble-bee) on its visit thrusts its proboscis into the narrow furrow between the two convexities on the lower lip, and forces these and the edges of the slit of the upper lip apart from each other; while Lindman maintains that the furrow in *P. recutita* is too narrow an opening for the introduction of the proboscis of the humble-bee, as this is not even possible in the larger-flowered *P. Oederi*, where the proboscis can only be thrust in higher up, at about the middle of the revolute portions of the edges of the upper lip ("die Rolle"). Visitors: Lindman observed *Bombus nivalis* and *Bombus alpinus*; Aurivillius mentions frequent visits of humble-bees.

According to Warming, fruit is set abundantly in Scandinavia.

Geographical Distribution. In the Carpathians and the Alps ("ganze nördliche Kette von St. Gallen bis Waadt — fehlt den Centralalpen," Schröter), the mountainous districts of Scandinavia, Arctic Russia and Siberia (recorded by Kjellman from several localities along the north coast of Siberia), Nova Zembla, Central Asia and the mountainous districts of East Asia.

Habitat: Blytt (Håndbog i Norges Flora) records

"boggy places in mountainous districts, ... from the birch-zone up to the lichen-zone; more rare below the pine-limit"; Th. Resvoll has now and then observed it in snow-troughs; it is, however, no typical snow-trough-plant. It does not ascend very high in the Alps; Schröter (p. 255) mentions it as occurring in the transition-zone between his Agrostidetum-trifolietum and Curvuletum (*Carex-curvula*-assoc.). In Arctic Eastern Asia Kjellman found it growing on damp coastal plains.

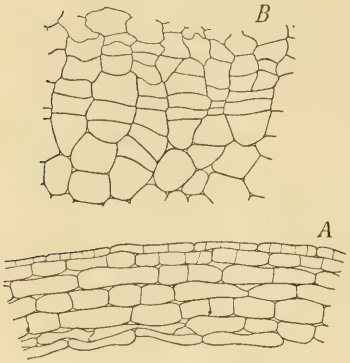

Fig. 45. *Pedicularis Oederi*. *A*, Transverse section of the peripheral layers of the root. *B*, Section through a leaf-scar. (*A* about $^{70}/_{1}$; *B* about $^{140}/_{1}$.)

Anatomy. In anatomical respects the root very much resembles that of *P. hirsuta*, the radiating cleft-formation in the stele — at any rate in the adventitious roots, which are the only ones that have been investigated — is not, however, so decided as in *P. hirsuta*.

The epidermis decays early; during growth the cells of the cortex are greatly elongated in a tangential direction, and undergo divisions by thin radial walls. The portion figured in Fig. 45, *A* is taken from a transverse section of an adventitious root, 6 mm thick; the endodermal region lies at a depth of only 3—5 cell-layers; the Casparian dots are still recognizable here and there in the endodermis, the cells of which, as those of the primary cortex, are seen to be very greatly elongated in a tangential direction, and to have undergone secondary division. In the secondarily formed cortex the parenchyma predominates over the sieve-tissue.

In all the parenchymatous cells of the root and meso-

corme (except the outermost layer) reserve food-material was found in the form of grains, as much as 10 μ in size, round, or slightly angular, and with a small central cavity. With a solution of iodine-iodide of potassum they assumed a red-violet to brownish-red colour, which disappeared on

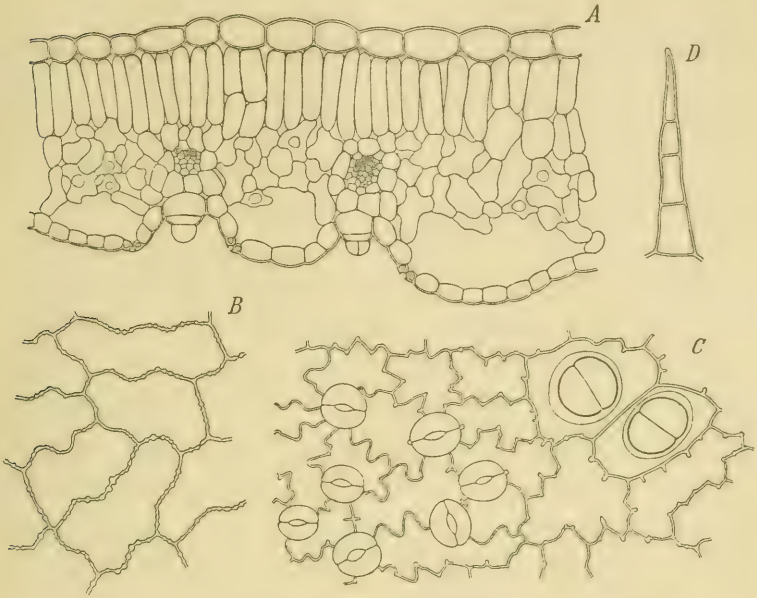

Fig. 46. *Pedicularis Oederi.*
A, Transverse section of the leaf. *B* and *C*, Epidermal cells, *B*, from the upper, and *C* from the lower surface of the leaf. *D*, A non-glandular hair. (*A* about $^{110}/_{1}$; *B* and *C* about $^{220}/_{1}$; *D* about $^{70}/_{1}$.)

heating, but reappeared after cooling; they stand out after treatment with potash-lye, and at last disintegrate altogether. Judging from the above-mentioned reactions, they must be assumed to consist of amylodextrin-starch.

The structure of the above-ground stem is fundamentally as in the other species. The thickening and lignification of the wood-fibres between and outside the vessels, and of the

peripheral cells of the pith, does not appear to take place until towards the time of ripening of the fruit.

The Leaf: Some of the cells of the upper and lower epidermis are shown in surface view in Fig. 46, *B* and *C*. Here, the great thickenings on the lateral walls of some of the epidermal cells of the upper surface and, as regards the lower surface, especially the walls of the cells which bear the glandular hairs, is very striking. This feature, however, is not constant in the species; as regards this point the individuals from Dovre were, on the whole, as shown in the figures in question, but the thickenings were far fainter, or even entirely wanting, in the specimens from Rörås. As usual in the *Pedicularis* spp. the stomata occur only on the lower surface of the leaf, and the epidermal cells which surround them have highly undulating lateral walls.

A transverse section of the leaf is shown in Fig. 46, *A*. The spongy parenchyma consists of copiously-branched cells, especially in its lower layer. As seen in the figure, the epidermis of the lower surface, in the spaces between the branches of the veins, is highly convex and in places without direct connection with the spongy parenchyma, so that, on the lower surface of the leaf, there are hollow spaces — air-chambers — in the roof of which the stomata occur. In the figure, a glandular hair is seen under each of the veins; two such hairs are shown in surface view in Fig. 46, *C*. *D* is a non-glandular hair. Chlorophyll-grains occur abundantly in the whole of the mesophyll, and in the epidermis of the lower surface.

A section through one of the scars which the leaves at their fall leave on the rhizome, showed that here a cork of at least six layers was formed; outside the leaf-scars no cork-formation takes place. A small portion of such a section is shown in Fig. 45, *B*.

Summary and General Remarks.

A. Account of the Growth-form and remarks on the Structure of the Shoot, the Vegetative Reproduction and the Winter-stage.

I. Undershrub-Chamæphytes: *Veronica fruticans* and *alpina*.

The shoot-development extends over 2 years; especially in *V. alpina* the first-year portions of the shoots often assume the character of runners; this, in conjunction with the abundant development of adventitious roots, and the dying away of the older portions of the stem, makes abundant vegetative reproduction possible in this species. Special bud-scales do not occur.

Both species may form lax tufts. Nanophyllous winter-greens. In the Arctic regions they require a snow-covering during their winter-rest; *V. fruticans* requires also a habitat which is freed from snow rather early in spring.

II. Hemicryptophytes.

a. Proto-hemicryptophytes: *Castilleia pallida* and *Bartschia alpina*.

The former species has a main root of long duration; in *Bartschia* it dies away early, and adventitious roots are abundantly developed; this in conjunction with the formation of runners allows rather abundant vegetative reproduction. When *Bartschia* grows in comparatively dry and firm soil the formation of runners is checked and it forms tufts; in that case it evidently forms a transition to the undershrub-chamæphyte type. Nano-microphyllous. During the winter-rest the growing-point is protected by the scale-leaves on the portion of the shoot formed the foregoing summer. In the Arctic regions *Bartschia* (and probably also *Castilleia*) requires a snow-covering during its winter-rest.

b. Rosette- or semi-rosette plants: *Pedicularis* spp.

1. With Runners: *P. lapponica* and *P. capitata.*

In *P. lapponica* the runners are most frequently monopodial, and during a limited number of growth-periods they form few-leaved rosettes at their apex, while the floral shoots, without any preceding vegetative stage, arise laterally on the rosette-axis. Sometimes the runners may terminate their growth by the formation of a floral portion. Floral shoots may also arise laterally on the basal portion of older shoots of the same kind, so that a small *rhizoma multiceps* is developed.

In *P. capitata* the runner terminates its growth after a vegetative period of 1—3 years, by the formation of a floral portion, often without foliage-leaves (a peduncle).

The winter-buds of both species are protected by scale-leaves. Adventitious roots are developed and vegetative reproduction takes place.

In the Arctic regions *P. lapponica* (and certainly also *P. capitata*) requires a snow-covering during its winter-rest.

2. Without Runners: *P. sudetica*, *euphrasioides*, *Sceptrum carolinum*, *hirsuta*, *lanata*, *flammea* and *Oederi.*

All these species have a short vertical rhizome ("mesocorme", E. Warming[1]); with reference to the duration of the main root, they may be divided into two groups, as stated by E. Warming (1890, p. 206 et seq.), viz., those in which it is of long duration, a fact connected with its vigour, and often rather copious branching (*P. euphrasioides*, *hirsuta* and *lanata*), and those in which it is of short duration (*P. flammea* and *Oederi*, to which may be added *P. sudetica* and *Sceptrum carolinum*).

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[1] E. Warming, 1918: Om Jordudlöbere (Underground Runners). With a résumé in English. Kgl. Danske Vid. Selsk. Skrifter. 8. Række. II. No. 6.

In those species in which the main root is vigorous and branched, the development of adventitious roots is repressed, and does not, at any rate, occur except in old individuals (cf. Th. Resvoll, 1917, p. 215); in the species of the other group adventitious roots are more or less abundantly developed, certainly according to the nature of the substratum. The length of the first vegetative-stage varies, as a rule, it may be of several-years duration. The variations must be assumed to be due to the varyingly favourable conditions afforded by the habitat in question, as for instance, early disappearance of snow in spring.

In *P. lanata* the winter-buds are protected by the large persistent bases of the foliage-leaves of the year's rosette; in the other species special bud-scales occur.

P. euphrasioides appears, perhaps exceptionally, to be able to occur as a biennial hapaxanth. The growth of the main shoot — in all the species which have been investigated — terminates by the development of a floral portion, frequently furnished with a few or several foliage-leaves, but sometimes quite devoid of these (individuals of *P. sudetica* and *Sceptrum carolinum*). The adventitious shoots arise most frequently in the axils of the scale-leaves; previous to their flowering they usually pass through a vegetative stage of some years duration. Only in *P. euphrasioides* the shoots usually appear to be able to achieve flowering in their second year. After fruit-setting the upper part of the shoot dies away; the complex of the persistent basal-portions forms a *rhizoma multiceps* (a mesocorme), which is especially large and vigorous when the main root is of long duration, as in *P. hirsuta* and *lanata*; these species also form the largest tufts.

In those species in which the main root and rhizome die away quickly behind, and adventitious roots are abundantly developed (especially in *P. sudetica* and *Sceptrum caro-*

linum) some vegetative reproduction takes place; but naturally by this means the plant can spread only to a very limited extent.

According to M. Porsild's observations *P. hirsuta* and *lanata* can dispense with a snow-covering during winter; all the other species of *Pedicularis* here mentioned no doubt require a snow-covering, but at the same time certainly also require that the snow in their neighbourhood shall melt rather early in spring; therefore, in the Arctic regions these species hardly belong to the real snow-trough flora, as is for instance the case with *P. hirsuta* in Norway. In southern Greenland, however, several of the species ascend rather far up the mountains (E. Warming, 1888, p. 87).

III. Therophyte: *Euphrasia arctica.*

Germinates in spring.

B. The Structure and Biology of the Flower.

In the large winter-buds of *P. sudetica*, *hirsuta*, *flammea* and *Oederi* the floral organs are found to be highly developed in the year previous to that in which they expand, and the same is probably the case in the rest of the species of *Pedicularis*. Also in *Veronica alpina* and *Bartschia alpina* floral organs have been demonstrated in the winter-buds.

The corollas are small and only slightly showy in *Veronica alpina* and *Euphrasia arctica*; in the former species the colour is deep blue, and in *Euphrasia* pale lilac to white, with yellow and violet markings. *Veronica fruticans* has bright blue corollas, which are even as much as 14 mm in diameter. *Bartschia alpina*, *Castilleia pallida* and the *Pedicularis* spp. have rather large flowers with brightly coloured corollas (deep bluish violet, red, yellow, and yellow with red or brown markings), collected into crowded and often large

inflorescences; *Bartschia* and *P. lapponica* have in addition coloured bracts.

Forms with white corollas have been found in *Veronica alpina*, *fruticans*, *P. hirsuta* and *lanata*.

Honey-secretion, either by a secretory ring around the ovary (*Veronica*) or by protuberances at its base, has been demonstrated in the majority of the species. Perfume is present in *P. lapponica*, *sudetica*, *euphrasioides* and *lanata*. The species which have been investigated varied from homogamous to slightly protogynous.

In *Veronica alpina* and *Euphrasia arctica* self-pollination is no doubt customary.

In the Arctic regions self-pollination no doubt plays an important part as regards the *Pedicularis* spp. since, according to several investigators (Ekstam, Porsild, etc.), insect-visitors are very scarce or even totally wanting there, and in Spitzbergen, as mentioned by Aurivillius, and as has since often been pointed out by others, none of the natural pollinators of these flowers (humble-bees) are found; in spite of this absence, *P. hirsuta* and *lanata* regularly set fruit there.

When, as in *P. flammea*, the stigma is always included in the helmet on account of the shortness of the style, cross-pollination by insects seems to be impossible. In *P. hirsuta* (no doubt frequently) and *lanata* (sometimes) the upper part of the style can be found to be so strongly curved that the stigma is pressed against the under-side of the anthers; perhaps this is due to movement which has taken place during a later stage in the flowering, so that originally cross-pollination has been possible; in the majority of the flowers of *P. lanata* which have been investigated, the stigma was found to protrude slightly beyond the tip of the helmet, as also in *P. sudetica*. In these three species the flowers are set almost horizontally, and the stigma is therefore placed under

the anthers, so that at any rate the dry and light pollen, when it falls out of the anthers by accidental shaking of the plant, will easily be able to fall upon the almost globular stigma. Self-pollination must take place with somewhat more difficulty in *P. euphrasioides* and *lapponica* owing to the great obliquity of the flower. The latter species, which has in addition the most protrusive stigma, is no doubt also the worst self-pollinator, and according to Porsild it is also the poorest fruit-setting species in Greenland.

In *P. Oederi*, in which the flower, as in *P. flammea*, stands almost in a vertical position, the upper lip curves forward and downward at the end of the flowering period, by which means the stigma is brought in a position that enables it to receive the pollen when it falls.

Pedicularis Sceptrum carolinum, as *Castilleia pallida*, no doubt normally requires insect-visits for pollination. *Bartschia alpina* is characterized by great variation in the length of its style; in the short-styled forms, especially in those in which the stigma is included in the helmet, self-pollination must easily be able to take place; any appreciable growth of the corolla tube has not been demonstrated in the Arctic regions, so the variations must be regarded as individual. On the other hand, in several instances of older flowers, the anthers were found to project outside the corolla so that in these cases we may perhaps assume with Kerner that some amount of cross-pollination takes place between older and younger flowers by the agency of the wind.

With the exception of *P. capitata* I found, in my material, ripe fruit in connection with all the species.

The seeds were small and light in all the species.

C. Parasitism.

As is well-known the *Euphrasia* spp., *Bartschia alpina* and the *Pedicularis* spp. are green semiparasites.

As regards their capability of assimilating the carbon dioxide of the air, Heinricher (1910, VI, p. 574) states that in the *Euphrasia* spp. this is almost normal, and the same author also attributes active assimilation to *Bartschia*. Volkart (1899, p. 30) sums up his results as regards the *Pedicularis* spp. (*P. recutita*, *foliosa* and *verticillata*) investigated by him as follows: "Die Versuche zeigen, dass die Stärkespeicherung der Blätter der untersuchten Pedicularisarten normal und ohne grosse Abweichung von denjenigen anderer Pflanzen vor sich geht. Eine weitgehende Herabsetzung der Assimilationstätigkeit durch den Parasitismus, wie sie Bonnier aus seinen Versuchen ableitet, findet nicht statt."

In this connection I wish to draw attention to the fact that the mesophyll, in all the *Rhinantheæ* spp. investigated by me, was found to be normal in structure, and its cells contained a normal supply of chlorophyll grains.

Bartschia alpina according to Heinricher's investigations, is an obligate parasite. According to Volkart, the *Pedicularis* spp. may show gradations in their dependency on other plants; from *P. palustris*, which he describes as "Stärkster Parasit mit stark entwickelter Neigung zur saprophytischer Ausnützung der Nährpflanze" (by the destruction of the roots attached), to *P. comosa*, which is said to be a "Relativ selbeständig entwichlungsfähige Art"; as regards *P. Oederi* he writes "Saprophytische und hydroparasitische Ausnutzung der Nährwurzel gleichgestellt."

From the Arctic regions we lack accounts of thorough investigations regarding this matter; but as regards *P. lanata* there is a note to hand which might suggest that under

certain circumstances this species may at times lead an independent life, since M. Porsild remarks (1920, p. 142) that he has found *P. lanata* growing "in gravelly barren, far away from other plants"; where it occurs among other plants, this species, also, has haustoria on its roots (l. c.).

According to Volkart, in the Alps the *Pedicularis* spp. do not appear to be very particular as regards host-plants. From the Arctic regions Rosenvinge and Warming records *P. hirsuta* and *flammea* as parasitic on *Vaccinium uliginosum* and *Salix herbacea*; Hartz (1905, p. 219) writes that in East Greenland *P. lapponica* "is closely connected with *Betula*, and probably occurs parasitically on its roots." A rather interesting circumstance connected with the present question is recorded by Chr. Kruuse (1911, p. 61) from the district of Angmagsalik. On some slopes facing north and cut into terraces, where a rich vegetation of "espalier-shrubs" was growing on the vertical sides of the terraces, he found the platforms to be "covered with coarse gravel which bore at great intervals (3—5 metres) wind-affected tufts of *Salix* (*Salix glauca*)", and in these tufts a *Pedicularis* (*hirsuta* or *flammea*) always occurred. "Where the platforms consist of sand, *Salix herbacea* is always predominant, and the latter also, with its crooked branches 5—10 cm long, protects a *Pedicularis*."

D. Anatomy.

The Root. Both the species of *Veronica* have a thin-walled, cuticularised exodermis; *V. fruticans* has a peripheral cork-formation in the root (as in the stem), whilst this is lacking in *V. alpina*. In both species the primary cortex persists a long time and, especially in *V. fruticans*, consists of rather thick-walled cells; the original endodermal cells are elongated during growth and undergo divisions by radial

walls which are quite thin in *V. alpina*, but of the same thickness as in the other cells of the cortex in *V. fruticans*. In the latter species there are distinct growth-zones in the xylem-portions of the stele, whilst such growth-zones are lacking in *V. alpina*.

It is common to the roots of *Euphrasia*, *Bartschia* and the *Pedicularis* spp. to have the primary cortex few-layered and its cells frequently very thin-walled; root-hairs are usually wanting (in some specimens of *Euphrasia arctica*, alone, I found a few scattered root-hairs).

In the species of *Euphrasia* the epidermis persists a long time; according to Hovelacque the same is the case in *Bartschia*, but in this I found that it may sometimes die away early. With the exception of *P. Sceptrum carolinum* it dies away very quickly in the *Pedicularis* spp. which have been investigated; even in roots a millimetre thick, I found the cells collapsed and partly thrust off; the outer walls of the layer below the epidermis become cuticularised, and where the growth in thickness of the root is considerable (*P. euphrasioides*, *hirsuta*, *lanata*, *flammea* and *Oederi*) the cells of the exodermis as well as of the other 3—6 layers of the primary cortex become greatly elongated tangentially and divided by thin radial walls.

The primary cortex persists a long time.

In *Bartschia alpina* and *P. capitata* a cuticularised lamella arises in the wall of the endodermal cells, in the former species all the way round, in the latter only in the inner and radial walls.

The Casparian dots were very distinctly discernable in *Euphrasia arctica*, and in *P. lapponica*, whilst they were quite faint in *P. hirsuta* and *lanata*.

Lacunæ, such as are found, for instance, in the primary cortex in *P. palustris* (Hovelacque), were, in the species

investigated, found well-developed in the adventitious roots of *P. sudetica* only.

In the roots of *P. Euphrasioides*, *hirsuta* and *lanata*, which had a vigorous growth in thickness, the rather thick secondary cortex was found to be traversed by radiating clefts (Fig. 38, *B*); this was less well-marked in the adventitious roots of *P. flammea* and *Oederi*. In *P. hirsuta* and *lanata* in which the thin-walled parenchyma — as is also the case in *P. flammea* and *Oederi* — is also dominant in the xylem, the clefts are often continued far into the latter.

In the xylem of *P. euphrasioides* distinct growth-zones were seen, each probably corresponding to one year's increment.

The thick roots and rhizomes in several of the *Pedicularis* spp. certainly contain a considerable amount of reserve food material, no doubt especially during the winter-rest; the sweet taste of these organs in *P. hirsuta* and *lanata* is well-known. In *P. flammea*, *Oederi* and in the specimen of *P. hirsuta* mentioned on page 462, which was collected in late summer, I found the roots full of amylodextrin-starch.

The condition of the material at my disposal did not allow of a closer study of the haustoria.

The Stem. As has frequently been pointed out (Hovelacque and Solereder) the absence of parenchyma-rays from the part of the xylem formed by the cambium, is a character widely distributed among the Scrophulariaceæ.

Parenchyma-rays were also absent from all parts of the shoot in the *Veronica* spp., *Castilleia pallida*, *Euphrasia* and *Bartschia alpina*, and from the above-ground parts of the axes in the *Pedicularis* spp. (in *P. lapponica* also from the runners). In these cases the cambium very quickly develops inwardly a continuous ring of vessels and wood-fibres, which bridges over the leaf-gaps so that these become demonstrable

on the inner side of the xylem-ring only as thinner portions of the latter among "les faisceaux reparateurs".

A transverse section of the rhizome in *P. sudetica*, *Sceptrum carolinum*, *hirsuta*, *lanata*, *flammea* and *Oederi* showed, on the other hand, a circle of vascular bundles mutually separated by parenchyma-rays, as is commonly the case in fleshy dicotyledonous rhizomes, especially such as are abundantly covered with leaves. With respect to *P. Sceptrum carolinum* this feature has been already described and figured by Chatin.[1] In *P. capitata* the runners had two rather broad diametrically opposite parenchyma-rays.

In the above-ground parts of the axes in the *Pedicularis* spp. the peripheral portions of the pith consisted usually of thickened, lignified and porose cells; this was most decidedly the case in *P. Sceptrum carolinum*, in the up to one-metre-high stem of which the stereom is, on the whole, very vigorously developed. When an elongation of the axis takes place during flowering and fruitsetting, the lignification of the stereom naturally does not begin until this is accomplished. The central portions of the pith are very thin-walled and die away early.

Hard bast was present in the periphery of the stele in *Veronica fruticans*, and very abundantly in the above-ground parts of the axis in *Bartschia alpina*; in the rhizome of the latter species the hard bast was present more sparingly, and sometimes totally absent.

Continued growth in thickness through several growth-periods could be observed in the persistent basal portions of the shoots of the two Arctic species of *Veronica* (in *V. fruticans* the growth in thickness is continued throughout many years — as many as 16 were counted), in *Castilleia*

[1] Chatin: Anatomie comparée des vegetaux. Plantes parasites. Dicotylédones. P. 192. Pl. XLII.

pallida (the increment was small and irregular) and sometimes in *Bartschia*; the runner-like portions of the shoots in *P. lapponica* occasionally show two annual rings; in the rhizomes in *P. Sceptrum carolinum* the xylem of the vascular bundles always showed two growth-layers, since in the second year of the rhizome-portion a group of vessels (and stereom) is developed outside that produced in the first year; the two groups are distinctly separated, some layers of thin-walled unlignified parenchyma being found between them. Thin-walled and unlignified cells are also present in the *Veronica* spp. at the boundary between the annual rings.

Cork-development occurs sub-epidermally in *Veronica fruticans* in the basal, persistent portions of the shoots, and in *P. Sceptrum* and *capitata* further within the primary cortex; the cork is always only few-layered, but *P. Sceptrum carolinum* develops, in addition, cork-cambiums in the parenchyma between the annual increments in the vascular bundles and also within the pith. In the majority of cases the endodermis was demonstrable by the presence of Casparian dots, or else a cuticularised lamella was found in its walls, either all the way round (as in the runners in *Bartschia*) or only on the inner and radial walls (runners of *P. capitata*).

The Leaf. All the species investigated have leaves mesomorphic in structure. The cuticle is thin; in *Veronica fruticans* a moderate thickening of the walls of the epidermal cells takes place, the other species have thin walls. The lateral walls of the epidermal cells of *Castilleia pallida* are almost straight, of the other species more or less decidedly undulating; in *Euphrasia arctica* and *Bartschia alpina* the difference between the epidermis of the upper and lower surfaces is in this respect inconsiderable; in the species of *Veronica* and *Pedicularis* I found that the epidermal cells of

the lower surface had the most decidedly undulating lateral walls.

The lateral walls of the epidermis in *Veronica alpina*, *Castilleia pallida* and *Euphrasia arctica* are without sculpture; in the other species they are porose; in *Veronica fruticans* and *Pedicularis euphrasioides*, *flammea* and *Oederi* the pores are distinct and alternate with flanged thickenings, whereas they are fine in *Bartschia alpina* and the other *Pedicularis* spp. It should be noted, however, that the epidermal cells of the lower surface which bear the large glandular hairs have (except in *P. lanata*) very vigorously developed flanged thickenings in the *Pedicularis* spp., and usually also in *Euphrasia* and *Bartschia*; also their walls are, on the whole, distinctly thicker than those of the surrounding epidermal cells.

Stomata occur exclusively on the lower surface of the leaf in the *Pedicularis* spp., nearly equally on both surfaces in *Veronica fruticans*, *V. alpina*, *Castilleia pallida* and *Euphrasia arctica*, and more abundantly on the lower surface in *Veronica officinalis* and *Bartschia alpina*. The guard-cells are on a level with, or raised only slightly above the leaf-surface; they are surrounded by 3—8 cells.

The mesophyll in all cases is rather lacunose and consists of thin-walled cells. In *Castilleia pallida* it may be almost homogeneous; 2—3 layers of short palisade-cells occur in the *Veronica* spp., *Euphrasia arctica* and *Bartschia alpina*. Of the *Pedicularis* spp., *P. euphrasioides*, *capitata*, *hirsuta*, *flammea*, *Oederi*, and frequently *lapponica*, had 1—2 layers of typically developed palisade-cells; they were shorter and broader in *P. Sceptrum carolinum*, *sudetica* and *lanata*.

In *P. flammea* and *Oederi* there were large air-chambers between the spongy parenchyma and the epidermis of the lower surface (cf. Fig. 46, *A*). In all the species investigated,

the cells of the mesophyll contained a normal number of chlorophyll-grains. In the majority of the cases chlorophyll-grains were also present in the epidermis of the lower surface.

Only *P. lapponica*, *Sceptrum carolinum* and *flammea* appear to be totally devoid of non-glandular hairs. The leaves were densely covered with hairs in *Castilleia pallida*, *Euphrasia arctica*, *Bartschia alpina*, *P. hirsuta*, *lanata* (in the last-mentioned two species especially along the edges of the petiole on the part near the base of the leaf) and *capitata* (on the lower leaf-surface and the petiole). The non-glandular hairs are from one to several-celled; in *Veronica fruticans* and *Pedicularis capitata* they are rather thick-walled, in the others thin-walled, smooth or with fine cuticular striations; only *Veronica fruticans* had hairs with coarser cuticular warts.

Glandular hairs were present in all the species: small glandular hairs with a one-celled stalk and two-celled head in the *Veronica* spp., *Castilleia pallida* and in especially great numbers in *Euphrasia* and *Bartschia alpina*; the last-mentioned two species had in addition large, peltate glands with a low sunk stalk-cell and a 2—4 celled flat head, like those in *Lathræa* (Scherffel, Haberlandt and Goebel; compare my Figs. 14 and 19). As previously mentioned by Hovelacque and Percy Groom, large glandular hairs of peculiar structure occur also in the *Pedicularis* spp.; here the low stalk-cell is not sunk, and the head is 2-celled (see for instance Fig. 23, *A* and *C*). All the species of *Pedicularis* which have been investigated had such glands.

The above-mentioned special forms of large glands are found only on the lower surface of the leaf and, as pointed out by the above-mentioned authors and as may be seen from my figure 24 and from most of the transverse sections of leaves figured, they are localised under the vein-branches

of higher order which at their tips consist only of a few thin-walled tracheids. According to information to hand it seems unquestionable that these glands are organs for the secretion of water.

As to the *Pedicularis*-glands it should be noted that special water-paths from the tracheids to the basal cell of the glandular hair, limited by the cuticularisation of cell-walls, as have been demonstrated in *P. palustris* by Percy Groom, have not been able to be demonstrated in any of the species investigated here. A bursting and crumbling-away of the cuticle on a small circular spot in the middle of the glandular head, such as the author in question mentions in connection with *P. palustris*, was very common in *P. lapponica* and *P. Sceptrum carolinum*, and was occasionally also found in other species.

Glandular hairs with a 2 to several-celled stalk and a 2—4 celled head were present in *Castilleia pallida*, *Euphrasia arctica*, *Bartschia alpina*, and also in *P. flammea*.

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